Invasion overlap: Abundance, diet, and interactions of two co-occurring invasive crabs (*Carcinus maenas* and *Hemigrapsus sanguineus*) in Nova Scotia, Canada.

by

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Abstract

Ecosystems increasingly harbour multiple invasive species, which can alter ecological interactions that influence their establishment, spread, and impacts on native communities. The recent arrival of the Asian shore crab to Atlantic Canada, where the European green crab has been well-established since the 1950s, provides an opportunity to examine how these invasive species interact during the initial stage of co-invasion in their newly shared range. This study examined their spatial co-occurrence and relative abundance at two sites in Nova Scotia during the summers (July/August) of 2022–2025 (quadrat sampling), along with diet analyses (stomach content) in 2022 and 2023. Follow-up experiments determined whether feeding and diet are altered by the presence of a competitor (alone vs. inter/intra-specific pairings). Both species were found in areas of <0.25 m^2. Green crabs were significantly more abundant than shore crabs (a single exception in 2025), indicating that the shore crab is still in the early stage of invasion. Both species are omnivorous generalists, consuming a variety of shared food items (12 species/taxa); however, the relative proportions of food items in crab stomachs differed between species and locations. Animal prey was predominant in green crab stomachs, whereas shore crabs contained a relatively high proportion of macroalgae. Similarly, green crabs were more likely to consume animal prey than macroalgae and vice versa for shore crabs. Green crabs altered their diet in the presence of shore crabs such that when paired with a shore crab, they were equally likely to consume either food item, but when alone or paired with a conspecific, they were more likely to consume barnacles. In contrast, shore crabs did not alter their diet in the presence of green crabs. These results are important for understanding how interactions among invasive species influence feeding and resource use, with implications for population and community dynamics.

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Introduction

Background

Contemporary ecosystems increasingly harbour numerous invasive species due to environmental and anthropogenic factors (e.g., climate change, natural migration, shipping traffic, and aquaculture) that create ideal conditions for a first introduction and potential secondary spread of non-native species (i.e., species transported beyond their natural biogeographical range; Soto et al. 2024) (Ruiz et al. 1997; Brousseau and Baglivo 2005; Green et al. 2011; Miranda et al. 2019). Herein, we define invasive species as established, non-native species that have recently spread or are rapidly expanding within their invaded range through active or passive processes, with or without human mediation, and irrespective of impact (Soto et al. 2024). While still in its infancy, research on multiple co-occurring invasive species indicates that they can have combined effects on ecosystems that differ from those caused by single invaders. The presence of multiple invasive species in an ecosystem can alter species interactions, thereby restructuring food webs, affecting population dynamics, and changing community composition and ecosystem function (e.g., marine: Griffen and Byers 2009; freshwater: Jackson et al. 2014; Fryxell et al. 2016; terrestrial: Lone et al. 2024; Hu et al. 2025). Consequently, understanding how invasive species interact where they co-occur is becoming increasingly important (Jackson 2015; Kuebbing and Nuñez 2015). For example, negative interactions between invasive species can lead to “serial replacement”, where one invasive species gradually displaces another and begins to dominate the community by outcompeting the other (Lohrer and Whitlatch 2002a; Jackson 2015). In contrast, positive interactions among invasive species can facilitate the establishment of additional non-native species through ecosystem-level effects (i.e., Invasional Meltdown Hypothesis; Simberloff and Von Holle 1999;

Catford et al. 2009). Additive effects occur when multiple invaders impact the ecosystem independently, with their combined impacts equaling the sum of their individual effects, such as the combined reduction of zooplankton by invasive zebra (*Dreissena polymorpha*) and quagga mussels (*D. rostiformis*) in North American lakes (Kissman et al. 2012). Alternatively, neutral interactions neither enhance nor inhibit the success of either invader (e.g., growth, survival, or spread), which may explain their coexistence in some ecosystems (Jackson 2015). Much of the research on the impacts of invasive species focuses on individual species, often overlooking co-occurring invasive species, and how their interactions affect each other and their combined effects on native species (Green et al. 2011), especially in marine ecosystems (Jackson 2015; Salimi et al. 2021).

Brachyuran crabs are among the most common and well-known invasive species in marine ecosystems, causing considerable ecological effects (Molnar et al. 2008). Concern about their impact is growing as new introductions and detections continue to increase worldwide (Howard et al. 2017). Two well-known marine invasive crabs with established populations outside their native ranges worldwide, occupying both geographically separate regions and ecosystems where their ranges overlap, are the European green crab (*Carcinus maenas,* Linnaeus 1758; hereafter green crab) and the Asian shore crab (*Hemigrapsus sanguineus*, De Haan 1853; hereafter shore crab).

The green crab is native to the Atlantic coast of Europe and Northern Africa and has established non-native populations along the western and eastern coasts of North America, as well as in South Africa, Australia, and East Asia (Klassen and Locke 2007). In North America, the green crab was first detected in Massachusetts, United States (USA) in 1817, likely introduced from southern Europe through the transport of adult crabs in dry ballast and ship hulls

(Klassen and Locke 2007). Since its initial introduction, the green crab has subsequently spread to eastern Canada, where it was found in the Bay of Fundy by the 1950s (Klassen and Locke 2007). A second, genetically distinct lineage originating from their native range in northern Europe was detected in northeastern Nova Scotia (NS) in the 1980s (Audet et al. 2003; Roman 2006). The secondary contact of these two lineages has resulted in the formation of a hybrid zone, spanning southern New Brunswick (NB) and southern NS (Jeffery et al. 2017; Lehnert et al. 2018), with hybrids also detected in Placentia Bay, Newfoundland in 2007 (Blakeslee et al. 2010; Jeffery et al. 2017). Along the east coast of North America, the green crab's current range extends from Virginia to Newfoundland (Grosholz and Ruiz 1996; Klassen and Locke 2007), and on the west coast, from California to British Columbia (arrived in ~1988) (Klassen and Locke 2007).

The shore crab is native to coastal rocky intertidal regions of East Asia, with established non-native populations along the Atlantic coasts of North America and western Europe (Klassen 2012; Epifanio 2013). In North America, the shore crab was first recorded in New Jersey (~1988) (Williams and McDermott 1990), likely introduced through ships' ballast water containing its pelagic larvae from northern Asia (Blakeslee et al. 2017; Bader et al. 2024). The shore crab was first observed in Canada in 2017 (Tucker Island, Yarmouth, NS), although it was not identified and officially reported until 2020 (Ramey-Balci 2021). The shore crab has also spread to parts of NB (unpublished data). In NS, it now extends along ~475 km of coastline with populations containing ovigerous females and multiple age classes (based on size), including new recruits (Ramey-Balci 2021). The distribution of these two invasive crabs now overlaps throughout the North Atlantic, spanning coastal areas from Virginia to Maine and into Canada (NS and NB).

Following its introduction to the east coast of the USA, shore crab population densities increased to levels exceeding those observed in their native range (maximum 55 ind./m^2 and 100 ind./m^2) (Fukui 1988; Klassen 2012) and it became the numerically dominant crab along much of the coastline with a concomitant decline in the invasive green crab populations (Lohrer and Whitlatch 2002a; Kraemer et al. 2007; O'Connor 2014, 2018). In some regions and at different stages of invasion, juvenile green crabs (15–35 mm carapace width [CW]; Mascaró and Seed 2001), and juvenile (<12 mm CW; Jungblut et al. 2018) and adult (12–40 mm CW; Jungblut et al. 2018; Kraemer 2019) shore crabs co-occur in the mid-to-high rocky intertidal zone at close spatial scales relevant for species interactions (e.g., within 0.25 m^2 and 1 m^2) (Jensen et al. 2002; Lord and Williams 2017). Shore crabs can displace other native decapods such as fiddler crabs (*Uca pugilator*; Peterson et al. 2014), and juvenile green crabs, through predation (Lohrer and Whitlatch 2002a), and direct and indirect competition for food, space, and shelter (Byers 2002; Jackson 2015; Baillie and Grabowski 2019; Móréh et al. 2024), which highlights possible ecological consequences of their co-occurrence.

Diet can play an important role in the success of invasive species, as establishment and spread may be partly limited by the availability of food resources (energy), emphasizing the importance of examining the diet of co-occurring invasive species (Norris et al. 2007; Calizza et al. 2021; Reese et al. 2023). Diets that promote growth can have significant consequences for the continued establishment and spread of invasive crabs (Belgrad and Griffen 2016). Crabs whose diet consists primarily of animal prey can lead to higher fecundity, long-term energy stores, and extended survival compared to crabs that feed on macroalgae (Griffen and Byers 2006; Belgrad and Griffen 2016; Reese et al. 2023). Differences in diet may result from species-specific foraging strategies, morphological constraints, ecological factors (e.g., habitat structure and

resource availability), dietary preferences, and competitive interactions (Chakravarti and Cotton 2014; Wilcox and Rochette 2015; Bleile and Thieltges 2021; Stumpp et al. 2021; Saborowski et al. 2023).

Existing studies on green and shore crabs from both native and non-native ranges indicate that they are opportunistic, generalist omnivores, consuming crustaceans (e.g., juvenile crabs, barnacles, amphipods), polychaetes, small molluscs (bivalves and gastropods), and macroalgae (Ropes 1968; Ledesma and O'Connor 2001; Baeta et al. 2006; Griffen and Mosblack 2011; Pickering and Quijón 2011; Blasi and O'Connor 2016; Bouwmeester et al. 2019; Cornelius et al. 2021); however, green crabs are more carnivorous, as indicated by stable isotope evidence from its native range (Helgoland; Saborowski et al. 2023). Analyses of shore crab stomach content often show a predominance of macroalgae and other algal material (invaded range: Lohrer and Whitlatch 1997; McDermott 1999; native: Saborowski et al. 2023), although availability of food in their environment can influence their diet (Brousseau and Baglivo 2005). Laboratory experiments have further demonstrated that although shore crabs may consume relatively more herbaceous material than green crabs, both species preferentially select animal prey (e.g., *Mytilus edulis*, *Semibalanus balanoides*) over macroalgae (e.g., sea lettuce: *Enteromorpha* spp. and red algae: *Chondrus crispus*) when given a choice (Brousseau and Baglivo 2005; Griffen 2011; Griffen et al. 2015). Both species of crabs, in their invasive range in Connecticut, are believed to have impacted the abundance of the commercially important native blue mussel (*Mytilus edulis*; Lohrer and Whitlatch 2002b) and reduced native barnacle (*Semibalanus balanoides*) abundances in field and lab microcosm experiments in New England (Tyrrell et al. 2006). The diet of the shore crab has not been examined in NS; however, Elner

(1981) and Wilcox and Rochette (2015) have examined the stomach content of green crabs in southwestern NS (Port Hebert) and the Bay of Fundy, NB

Interspecific interactions between co-occurring invasive crabs can alter their feeding and diet (Jensen et al. 2002; Griffen et al. 2008). For example, MacDonald et al. (2007) found juvenile invasive green crabs outcompeted invasive adult shore crabs and native adult blue crabs (*Callinectes sapidus*) for a bivalve (ribbed mussel: *Geukensia demissa*), with green crabs being the quickest to locate and consume it under experimental laboratory conditions. Additionally, laboratory and field experiments have shown that, during direct competition, shore crabs can alter the diet of the green crab (Griffen et al. 2008). Likewise, intraspecific interactions among green crabs can also affect feeding by significantly reducing foraging and handling times (Chakravarti and Cotton 2014), and previous field experiments have shown intraspecific interactions between invasive adult green and shore crabs leads to more aggressive behaviours than interspecific ones (Griffen 2006; Griffen and Williamson 2008).

Ecological impacts and competitive outcomes can be context-dependent, depending on the environment, ecological conditions (Byers 2002), or even the time since first introduction (Crooks 2005) and the duration of co-occurrence. For example, invasive species may undergo temporal changes in resource use, morphology, physiology, or behaviour through acclimatization to their environment (fruit fly: *Drosophila malerkotliana*: Parkash et al. 2014; saltmarsh cordgrass: *Spartina alterniflora*; Liu et al. 2019; Pacific oyster: *Crassostrea gigas*; Kinnby et al. 2025). Investigating interactions across various habitats and invasion stages is essential for predicting the effects of invasions and informing effective management strategies.

Objectives

The overall goal of my research is to examine fine scale patterns of co-occurrence, relative abundance, diet, and the interactions of green and shore crabs in NS where the shore crab has recently become established and is spreading (first observation in ~2017; Ramey–Balci 2021) and co-occurs with the green crab which has been established for over seven decades. The relative abundance of these crabs will be used to estimate the stage of invasion of shore crabs, as described by O'Connor (2014). By investigating the diets of the shore crab and green crab in intertidal areas of NS through field surveys and using this diet information to inform controlled experiments, I address knowledge gaps in their resource use and potential competition for food in the intertidal ecosystem of NS. Assessing both crabs' relative abundance over time and space, and how inter- and intraspecific interactions influence feeding and diet, can enhance our understanding of their impacts on native intertidal communities and the population dynamics of these co-invaders.

My specific research objectives are to: (1) Determine if the shore crab and green crab co-occur at small spatial scales relevant for species interactions. Interactions such as competition, aggression, or feeding interference typically occur at small spatial scales (Yamada and Boulding 1998; Cannicci et al. 2018). Because rocky intertidal habitats often contain high abundances of resources such as food and shelter used by both species of crabs, I expect that these crabs will co-occur at small spatial scales (<0.25 m^2). (2) Examine the relative abundance of shore crabs and green crabs over time and space to determine their stage of invasion. Based on O'Connor (2014), I will determine the stage of the shore crabs invasion by examining the relative abundances of these species, with "early" (the green crab is significantly more abundant than the shore crab – statistically), "middle" (both species have similar abundances – not significantly

different), and “late” stages of invasion (the shore crab is significantly more abundant than the green crab). (3) Determine if there are interspecific differences in diet between species and sites over two years. I predict that both species will feed on similar food resources; however, the relative proportion of food items in stomachs will differ among species and sites. I expect that animal prey will make up the highest proportion of food items in both species’ stomachs; however, the shore crab will generally contain a higher proportion of macroalgae than the green crab. (4) Compare the feeding and diet in the presence of a competitor. I hypothesize that feeding and diet are altered in the presence of a competitor, and inter- and intraspecific interactions affect foraging and diet differently. While together, crabs may engage in numerous types of interactions (e.g., agonistic behaviour and interference competition) that reduce the time available for feeding and foraging (Lohrer and Whitlatch 2002a; Griffen 2006; Chakravarti and Cotton 2014). Interspecific interactions have less impact on foraging and feeding compared to intraspecific interactions (Griffen and Williamson 2008). Therefore, the likelihood of food in crab stomachs is expected to be lower when crabs forage together than when foraging alone. Additionally, the likelihood of food being present in crab stomachs (presence/absence) is expected to be lower when crabs are paired with conspecifics (same species) than heterospecifics (different species). Moreover, since green crabs have been shown to dominate interactions with shore crabs in preliminary field experiments in NS (DeJaegher et al. in prep) for bivalve prey (*Mytilus edulis*), similar to what MacDonald et al. (2007) observed in their experiments, green crabs are expected to be the stronger competitor, such that when alone, both crabs are more likely to have high-quality animal prey (barnacle) compared to macroalgae in their stomachs; however, when foraging together, shore crabs are more likely to consume macroalgae.

Methods

Fine scale patterns of co-occurrence and abundance

Crab surveys were conducted in the mid-to-high intertidal zone at two field sites in southwestern NS distributed in the inner (Doty Rd.; 44.4792, -65.9799) and outer (Cape St. Mary's; 44.0847, -66.2080) areas of St. Mary's Bay (Figure 1) over four field seasons (July and August) (Table 1). To measure crab density, quadrats (0.5 x 0.5 m; area 0.25 m^2) were placed in the mid-high intertidal zone, 1–2 m apart parallel to the shoreline at each site. Within each quadrat, the rocks, seaweed, and the top 2 cm of sediment were moved to expose and collect crabs. All crabs were identified, counted, sexed, and measured for carapace width (CW). CW was measured at the two widest points of the carapace, between the second and third anterolateral teeth (Delaney et al. 2008), using digital calipers to the nearest 0.01 mm.

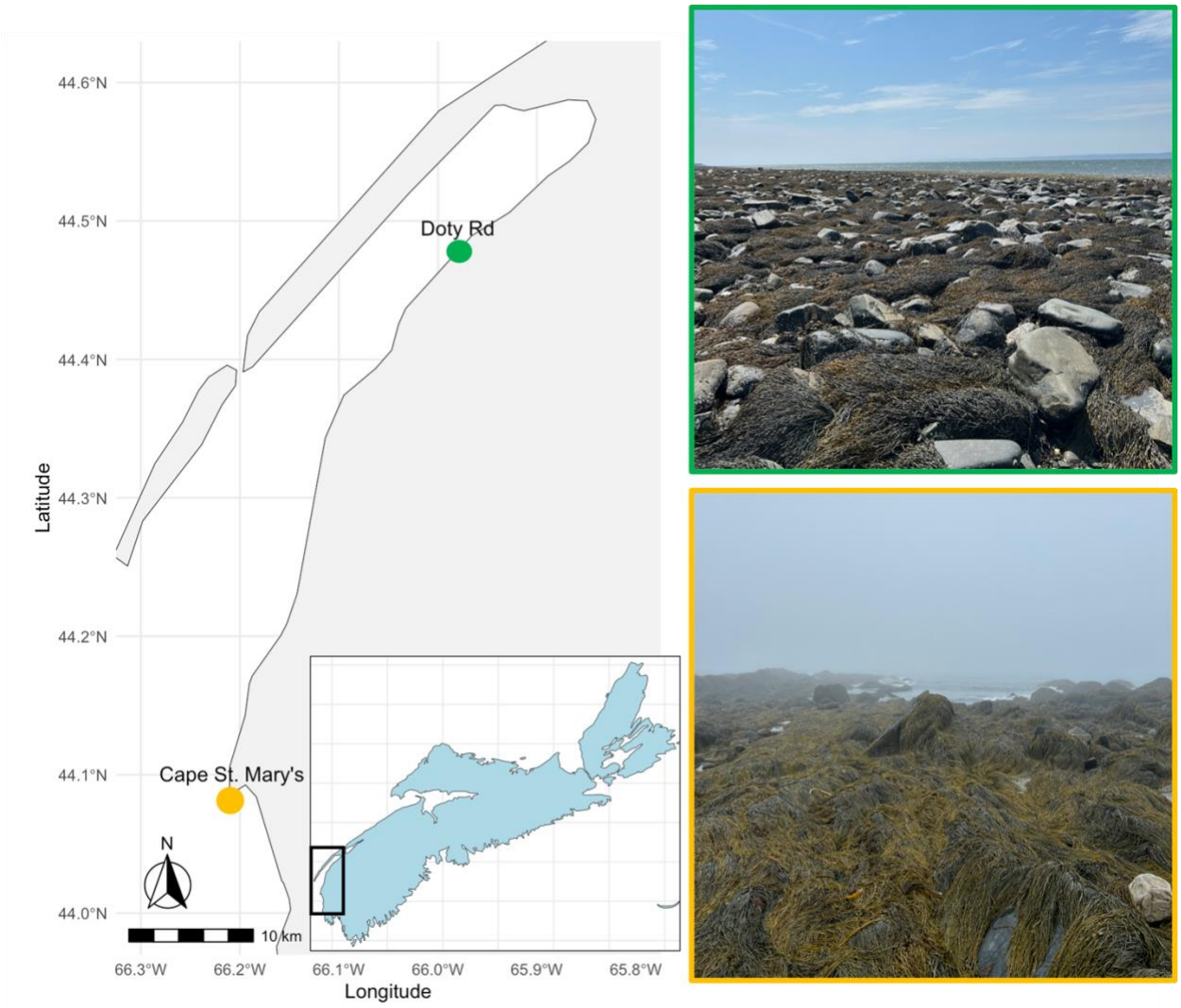


Figure 1. Field sites where crab surveys were conducted in St. Mary's Bay, Nova Scotia, in July 2022 to 2025. Smaller inset indicates the location of St. Mary's Bay in Nova Scotia. Symbol and image border colours indicate, green: Doty Rd. (44.4792, -65.9799) and orange: Cape St. Mary's (44.0847, -66.2080).

Table 1. Crab survey sites used to determine the spatial distribution and relative abundance of crabs in St. Mary's Bay, Nova Scotia including the year and date the survey was conducted and the number of quadrats (*n*) (0.5 × 0.5 m; area 0.25 m²) used.

Site	**Year**	**Date**	**Quadrats (*n*)**
Doty Rd.	2022	July 12, 13	28
	2023	July 16, 26	36
	2024	July 15	34
	2025	August 1	18
Cape St. Mary's	2022	July 14	36
	2023	July 20	36
	2024	July 16	36
	2025	August 3	18

Diet

Crabs used for diet analysis were collected in the mid-to-high intertidal zone at Doty Rd. and Cape St. Mary's in July 2022 and 2023, by haphazardly lifting rocks and macroalgae to expose crabs (2022: green crabs n = 153, shore crabs: n = 76; 2023: green crabs n = 50, shore crabs: n = 40). Crabs were identified, sexed (i.e., by looking at the shape of the ventral abdominal flap), and counted. Crabs were collected at dawn on receding tides. This approach increases the likelihood of obtaining full stomachs with minimal digested content, given that crabs typically feed at night (Mathews et al. 1999; Reese et al. 2023). Crabs were euthanized by freezing at -20°C before dissection and fixation of stomachs in a 70% ethanol solution. Food items consumed were identified and quantified under a ZEISS stereomicroscope to the lowest possible taxonomic level based on recognizable key structures (often fragments or larger pieces) that would allow the identification of prey, such as shells (barnacles and bivalves), opercula of gastropods, setae and jaws of polychaetes, macroalgae, appendages and carapace of crustaceans (see Table 5). Unidentifiable, highly digested material was categorized as detritus. The proportion (%) of each food item in each stomach was determined by counting the number of grid squares (3 x 3 mm) occupied by that item on a gridded petri dish, relative to the total number of grid squares covered by the entire stomach content (minus those covered by detritus) (Figure 2). Care was taken to evenly spread food items in a single layer on the grid to ensure consistency among samples. Following removal of empty stomachs (defined as having no food or < 1 square of food), a total of 235 crabs (green crabs: n = 153, shore crabs: n = 82) for 2022 and 2023 were used for subsequent diet analysis (Table 2). Additionally, any food items that were not found in at least 10 crab stomachs were removed from analyses.

Table 2. Number of green (GC) and shore (SC) crabs collected for diet analyses at Doty Rd. and Cape St. Mary's in 2022 and 2023. Values include number of stomachs with food present (stomach content covered < 1 square on grided petri dish), number of male (M) and females (F) and the mean carapace width (CW) ± the standard error (SE).

Species and site	**Year**	**Total no. crabs collected**	**No. stomachs with food**	**No. males and females**	**CW ± SE (mm)**
GC Doty Rd.	2022	71	49	M = 20 F = 29	28.96 ± 1.261
GC Cape St. Mary's		82	67	M = 26 F = 41	28.98 ± 1.042
SC Doty Rd.		23	17	M = 9 F = 8	20.81 ± 0.708
SC Cape St. Mary's		61	38	M = 22 F = 16	18.34 ± 0.517
GC Doty Rd.	2023	22	16	M = 5 F = 11	29.68 ± 2.247
GC Cape St. Mary's		28	21	M = 9 F = 12	24.37 ± 0.925
SC Doty Rd.		16	9	M = 3 F = 6	18.55 ± 1.345
SC Cape St. Mary's		24	18	M = 11 F = 7	19.03 ± 0.658

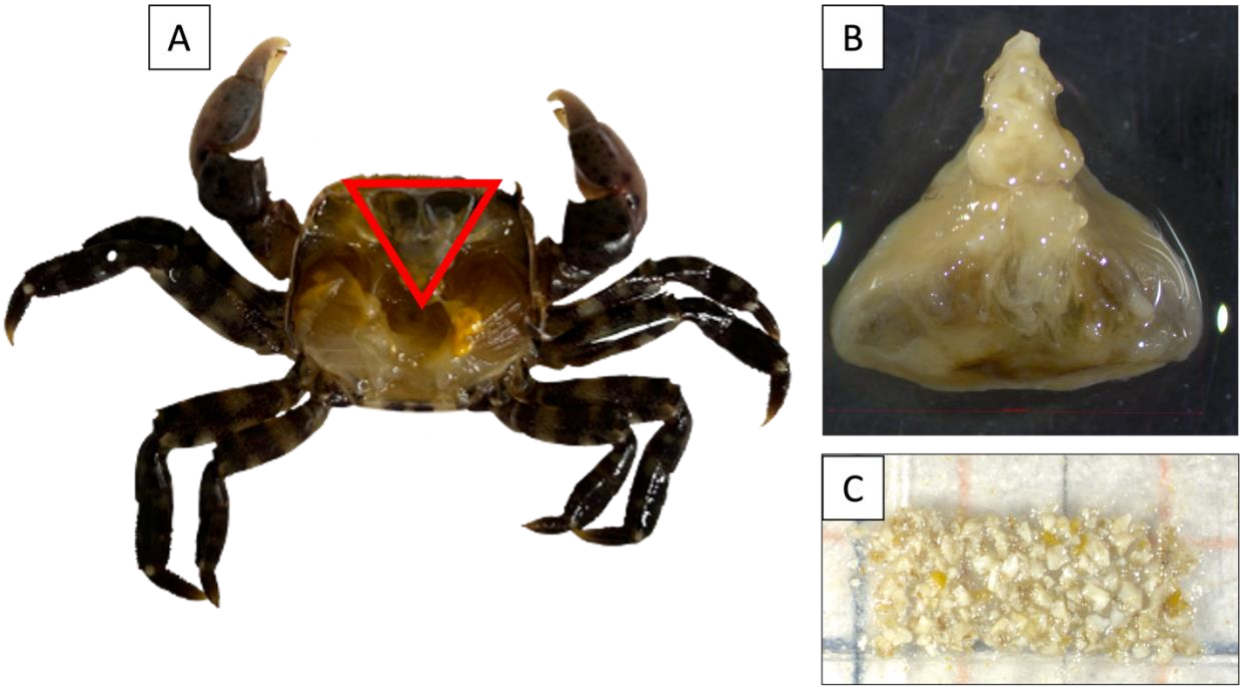


Figure 2: (A) Asian shore crab with dorsal carapace removed, showing the stomach (red triangle), (B) fixed stomach under a stereomicroscope, and (C) stomach content including barnacle (white) and macroalgae (light brown) evenly spread over a 3 x 3 m grided petri dish.

Feeding experiments

Field collection and handling of crabs

Crabs for feeding experiments were collected between July 16 and 30 of 2024 and July 22 in 2025, from the mid-to-high intertidal zone of two sites (Doty Rd. and Cape St. Mary's) in St. Mary's Bay, NS (Figure 1). Experiments included adult male shore crabs (CW: 14.58–23.93 mm, 19.02 mm ± 0.28, n = 64) and juvenile green crabs (CW: 17.58–36.37 mm, 27.46 mm ± 0.58, n = 52).

Only male crabs in the calcified intermoult stage with hard carapaces and having all their claws (chelae) and legs were used in experiments (also see Griffen et al. 2008; Karlsson et al. 2019; Bouwmeester et al. 2019). Female crabs were not used in experiments given that adult female shore crabs are commonly ovigerous during July which may affect foraging behaviour since gravid females tend to have lower metabolic rates, which may be a proxy for lower feeding rates (Neu et al. 2025). Green crabs in experiments only included the green colour morph (no red).

Experimental design

To compare feeding and diet, experimental arenas were set up containing two contrasting food sources including a high-quality animal prey (barnacle) and lower quality macroalgae (Figure 3A, C). Experimental treatments included: One shore crab alone (n = 16), one green crab alone (n = 16), both species together (n = 28), two shore crabs together (n = 17), and two green crabs together (n = 11).

Preliminary examination of crab stomach content indicated that both food items were commonly consumed by crabs at my field sites. Each arena across treatments contained similarly sized rocks with small barnacles (*Semibalanus balanoides*) and brown macroalgae (equal

mixture of *Fucus vesiculosus*, *F. spiralis*, and *Ascophyllum nodosum* secured with a zip tie). Each food item was placed at opposite ends of the arena (Figure 3D, E, F, and G). Preliminary experiments confirmed that crabs consumed both food items and did not exhaust either resource under any of the treatment conditions (indicated by about 50% food remaining after trials, determined qualitatively). Each arena was filled with filtered seawater (filter: 63 µm mesh; water depth: ~6 cm; 16–18°C) and randomly placed along a transect every 2 m to ensure independence among treatments (Figure 3B).

Experimental protocol

To standardize hunger levels and clear crab foreguts (McGaw and Curtis 2013; Bouwmeester et al. 2019), crabs were held separately in individual cages (filtered seawater, 63 µm mesh) for 24 hours prior to experiments. Since equally sized competitors are expected to have the greatest impact on foraging behaviour (Karlsson et al. 2019; Bleile and Thieltges 2021) crabs in same treatment were size matched (i.e., having similar CWs). Crabs for alone and heterospecific treatments were systematically placed on opposite sides of the experimental arenas (40 L x 31 W x 14 H cm bins), whereas crabs for conspecific treatments were haphazardly placed (Figure 3). Trials began between 9:00 and 9:15 PM (between July 21 and 31, 2024 and July 26, 2025), and crabs were left to feed for one hour, a time chosen to avoid stomach clearance (between 1 and 12 hours in green crab; McGaw and Penney 2014). Following the experiment, crabs were promptly euthanized, and stomachs were removed and fixed in a 70% ethanol solution. Stomach content was examined under a stereomicroscope and categorized by the presence/absence of food items (i.e., no food, macroalgae present, barnacle present, or both food items present).

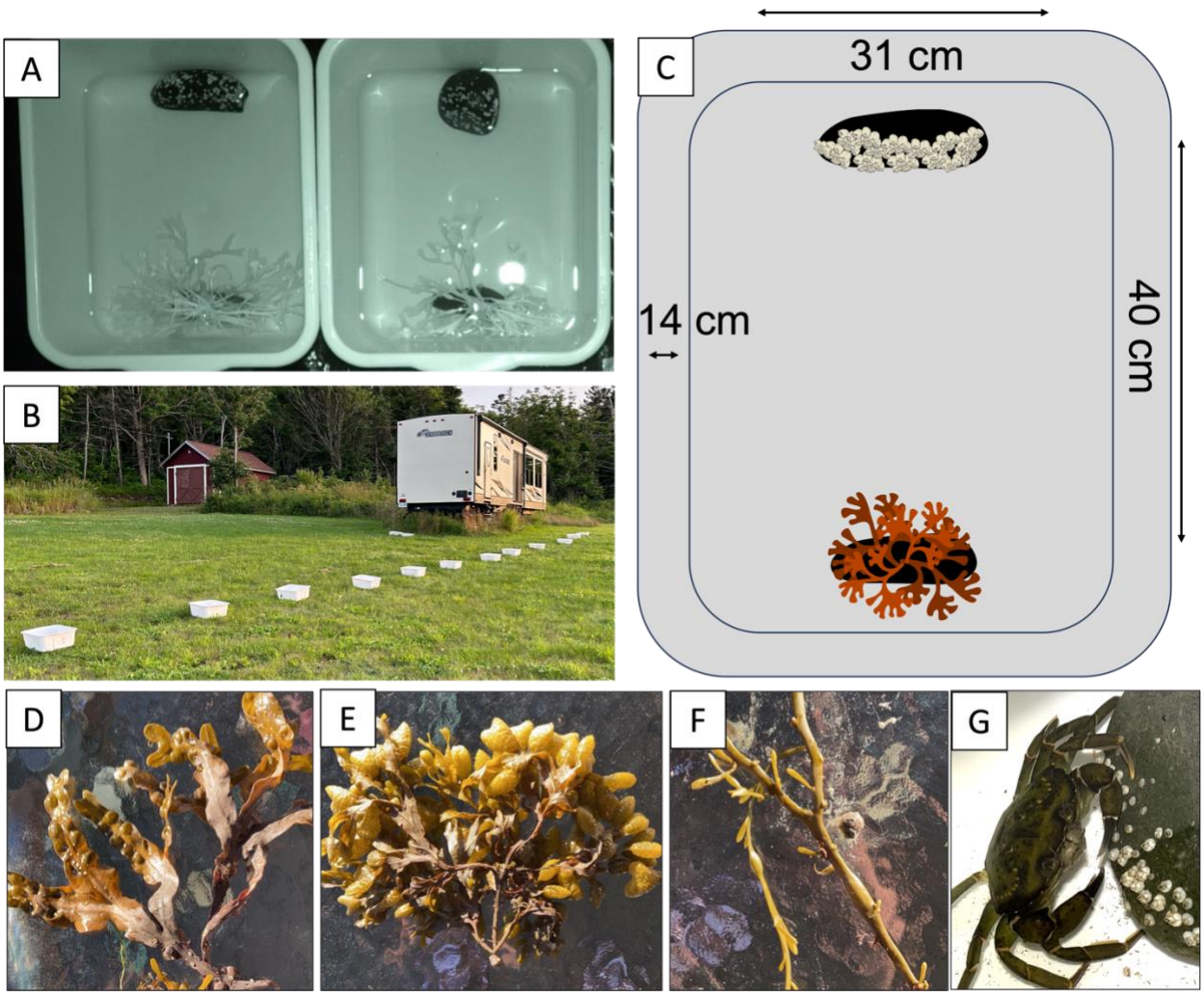


Figure 3: Experimental design for feeding experiments (A–C). Experimental arenas (A) with filtered seawater (image taken under infrared light), B) placed 2 m apart along a transect outside prior to nighttime experiment, and (C) diagram showing the dimensions (40 L x 31 W x 14). Food items included: (D) *Fucus vesiculosus*, (E) *Fucus spiralis*, (F) *Ascophyllum nodosum*, and (G) *Carcinus maenas* feeding on *Semibalanus balanoides*.

Data analyses

Fine scale patterns of co-occurrence and abundance

To examine patterns of crab occurrence within quadrats, the frequency of crab aggregations was examined in two ways, first by considering all crabs (i.e., including new recruits and juveniles < 12 mm; see Appendix) and then only considering crabs with a CW > 12 mm. Frequency of aggregations was calculated by tallying each category (no crabs, one green crab, one shore crab, multiple green crabs, multiple shore crabs, and both species together) and dividing these counts by the total number of quadrats. Larger individuals and adults (CW > 12 mm) were examined because these size classes are more likely to overlap in resource use and engage in direct competition, as examined herein.

To determine the stage of invasion, green and shore crab densities (response variable) were compared at each site (Doty Rd. and Cape St. Mary's; independent variable) and year (2022 to 2025; independent variable) using paired t-tests when data met assumptions of normality and equal variance. Data were assessed for normality using the Shapiro-Wilk test and homogeneity of variance using Levene's test. Prior to running the paired t-tests, all data were square-root transformed to meet model assumptions; however, the 2025 data from Doty Rd. did not meet the assumptions of normality or equal variance and could not be normalized through transformations (i.e., square root transformed); instead, a Wilcoxon signed-rank test (non-parametric) was used. These analyses were conducted using JAMOVI 2.3.28.

Diet

To visualize interspecific differences in diet across sites and years, a Principal Coordinates Ordination (PCO) analysis was performed using PRIMER (v7 + PERMANOVA) (Anderson 2001, 2017; Clarke and Gorley 2015). The PCO was conducted on a Canberra (D10) dissimilarity matrix generated from the relative proportion of species/taxa found in crab stomachs (response variable) separately for each year (*n* total 2022 = 171; *n* total 2023 = 64). Prior to analysis, proportions were log (x + 1) transformed to reduce the relative influence of the more abundant food items, which would otherwise dominate the dissimilarity matrix (Clarke and Gorley 2015). A Canberra dissimilarity matrix was used (rather than Bray-Curtis dissimilarity) to overcome arch effects observed in the exploratory analysis of PCO (Podani and Miklós 2002; Komendić et al. 2023). Vector overlays were used to show the species/taxa most important in driving the observed differences in crab stomach content (based on Pearson correlation, $p \geq 0.6$). Given the substantial difference in sample size between 2022 and 2023, separate Permutational Multivariate Analysis of Variance (PERMANOVA) were conducted for each year to avoid a highly unbalanced multifactor model with complex higher-order interactions. Within each year, differences in diet among sex, species, and sites (independent variables), as well as interactions, were tested using PERMANOVA (PRIMER; v7 +PERMANOVA; 9999 permutations). This analysis tested the null hypothesis that the centroids (equivalent to the mean in univariate analysis) of stomach content composition (i.e., proportion of species/taxa) did not differ among factors or their interactions. Since the design within each year remained somewhat unbalanced, Type III Sum of Squares (SS) was used to evaluate each main effect and interaction after accounting for all other terms (Anderson et al. 2008). Homogeneity of dispersion among factor levels was assessed using PERMDISP to determine whether significant PERMANOVA results

reflected differences in group centroids rather than differences in dispersion. Significant interactions were further examined with post-hoc pairwise comparisons to determine which factor levels and combinations of factor levels differed (only relevant comparisons are presented).

Species interactions

To compare feeding and diet in the presence of a competitor, a Generalized Linear Model (GLM: binomial distribution, logit link) was used to test whether species, treatment, or their interaction (independent variables) affected the presence of food, barnacle, or macroalgae (response variables) in crab stomachs. A Generalized Mixed Model (GMM: binomial distribution, logit link, crab IDs entered as random effects on the intercepts) was also used to test whether the presence of a food item (response variable) differed across treatments (independent variable: food types, treatments) separately for each species. To account for repeated measurements on the same individual (i.e., presence/absence of barnacle and macroalgae in each crab stomach content), crab IDs were included as a random effect. Post-hoc tests for planned comparisons (i.e., determined prior to analysis, based on hypotheses) were used to assess whether the presence of barnacles versus macroalgae differed for each treatment. JAMOVI 2.3.28 statistical software was used for all analyses.

Stacked bar graphs were used to examine differences in the proportional composition of stomach content (i.e., no food, presence of barnacle, presence of macroalgae) among treatments (i.e., alone, conspecific, heterospecific) for both species. For each species and treatment, stomachs containing both food types were assigned to both barnacle and macroalgae categories. Counts for each category were then summed within treatments and converted to proportions by

dividing by the total counts across all three categories. These proportions were expressed as percentages to compare among treatments.

Results

Fine scale patterns of co-occurrence and abundance

The density of green crabs was significantly higher than shore crabs at both sites over all years, except for Doty Rd. in 2025 (Table 4 and Figure 5). The average CW of crabs residing in the mid-high intertidal zone at Doty Rd. and Cape St. Mary's across all years is provided in Table 3. The mean CW (±SE) at Doty Rd was 21.49 ± 0.57 mm for green crabs and 18.49 ± 0.55 mm shore crabs. At Cape St. Mary's, the mean CW was 19.51 ± 0.31 and 14.88 ± 0.36 for green and shore crabs, respectively. The number of green crabs with CW > 35 mm at Doty Rd. and Cape St. Mary's across all years was 20 and 4, respectively (Table 3). Across all years at both sites, aggregations of multiple individuals were frequently observed in 0.25 m^2 quadrats, particularly heterospecific aggregations of green and shore crabs (GS) and conspecific aggregations of green crabs (GG) (Figure 4). In comparison, conspecific aggregations of shore crabs (SS) and single individuals of either species (G or S) were observed infrequently. The frequency of empty quadrats (no crabs) was low at both sites across years.

Table 3. Size of green and shore crabs at Doty Rd. and Cape St. Mary's in July/August of 2022 to 2025 including the number of crabs (*n*), minimum and maximum carapace width (CW) with number of green crabs ≥ 35 mm (CW / no. green ≥ 35 [mm]), and mean carapace width (CW mean ±SE [mm]).

Site	**Species**	**Year**	***n***	**CW / no. green ≥35 (mm)**	**Mean ±SE (mm)**
Doty Rd.	Green crab	2022	107	7.89 – 47.59 / 6	20.99 ±0.92
		2023	119	<1.00 – 45.8 / 6	16.33 ±1.06
		2024	150	6.37 – 48.37 / 7	16.59 ±0.77
		2025	21	11.06 – 36.53 / 1	22.66 ±1.67
	Shore crab	2022	22	5.80 – 24.73	18.83 ±1.13
		2023	25	4.79 – 23.25	12.69 ±1.70
		2024	23	5.63 – 27.02	16.82 ±1.00
		2025	8	13.26 – 21.66	19.43 ±1.09
Cape St. Mary's	Green crab	2022	759	3.44 – 38.96 / 2	9.69 ±0.21
		2023	325	4.61 – 30.28 / 0	11.92 ±0.58
		2024	314	3.20 – 47.16 / 1	12.85 ±0.51
		2025	118	6.75 – 37.07 / 1	16.98 ±0.65
	Shore crab	2022	61	3.44 – 22.37	14.76 ±0.65
		2023	41	8.40 – 22.98	15.04 ±1.16
		2024	106	1.35 – 24.14	12.43 ±0.54
		2025	36	8.85 – 21.45	15.77 ±0.59

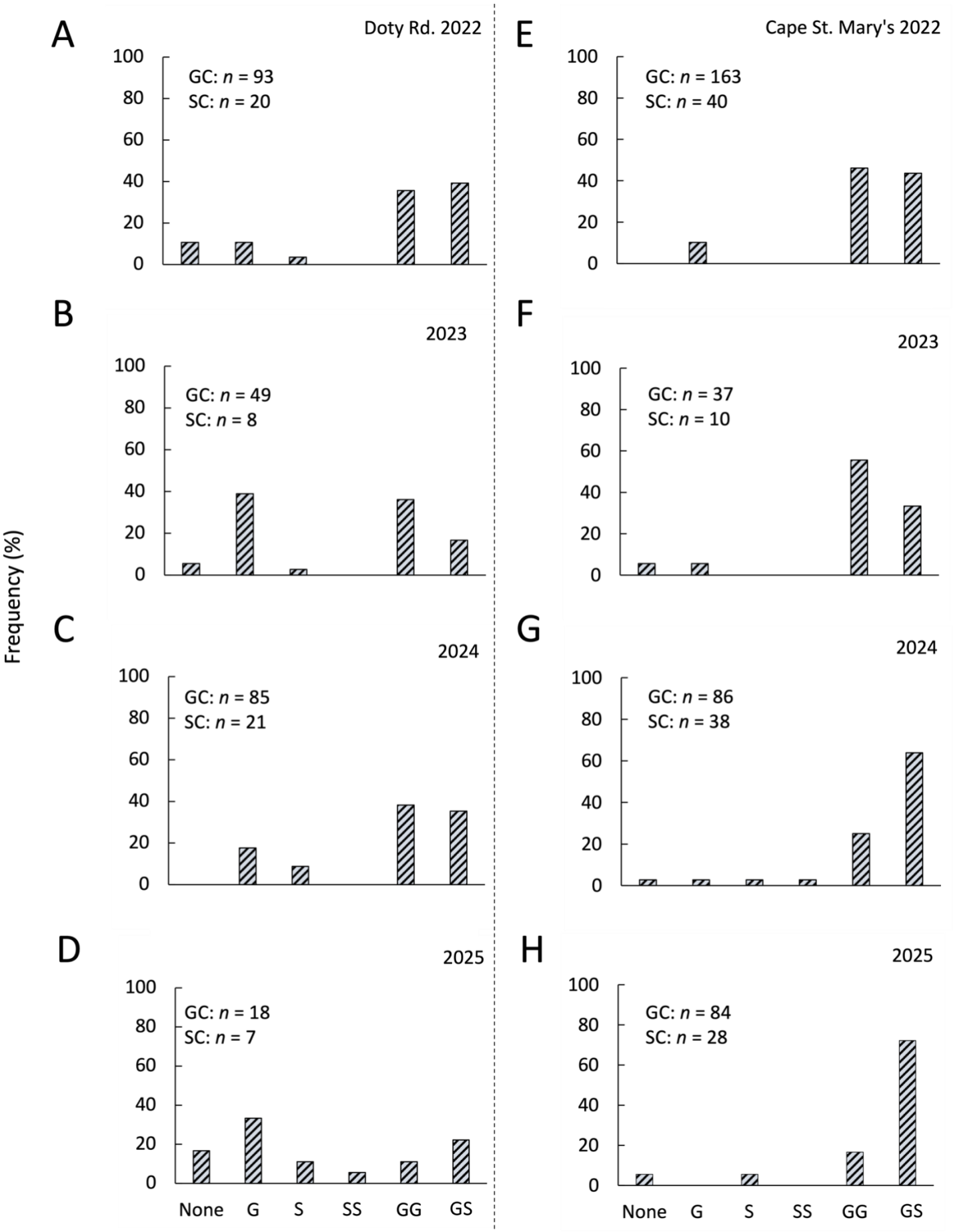

A
Doty Rd. 2022
GC: n = 93
SC: n = 20
B
2023
GC: n = 49
SC: n = 8
C
2024
GC: n = 85
SC: n = 21
D
2025
GC: n = 18
SC: n = 7
E
Cape St. Mary's 2022
GC: n = 163
SC: n = 40
F
2023
GC: n = 37
SC: n = 10
G
2024
GC: n = 86
SC: n = 38
H
2025
GC: n = 84
SC: n = 28
Frequency (%)
0
20
40
60
80
100
None
G
S
SS
GG
GS

Figure 4. Frequency (%) of all crab occurrences in 0.25 m^2 quadrats by category at Doty Rd. (left panels) and Cape St. Mary's (right panels) in July/August of 2022 to 2025. Crabs with carapace width < 12 mm were removed. Categories: none (no crabs), G (one green crab), S (one shore crab), SS (multiple shore crabs), GG (multiple green crabs), and GS (both green and shore crabs). Each panel includes total number (*n*) of green crabs (GC) and shore crabs (SC) collected during quadrat sampling. Table 1 indicates number of quadrats for each site/year.

Table 4: Results of statistical tests comparing green crab (GC) and shore crab (SC) densities for each site/year. Values reported include the test statistic (Student's *t* or Wilcoxon signed-rank test, *W*), degrees of freedom (df), *p*-value, and effect size (Cohen's *d* or rank biserial correlation, RBC). Bold *p*-values represent significant differences between green and shore crab densities for each site/year.

Site/Year	**Test statistic**	**df**	***p*-value**	**Cohen's *d* or RBC**
Doty Rd. 2022	$t = 5.60$	27	**<0.001**	1.060
Doty Rd. 2023	$t = 7.05$	35	**<0.001**	1.170
Doty Rd. 2024	$t = 8.67$	35	**<0.001**	1.450
Doty Rd. 2025	$t = 1.38$	17	0.185	0.326
Cape St. Mary's 2022	$t = 13.6$	35	**<0.001**	2.260
Cape St. Mary's 2023	$t = 9.25$	35	**<0.001**	1.540
Cape St. Mary's 2024	$W = 533$[a]	35	**<0.001**	0.900
Cape St. Mary's 2025	$t = 4.32$	17	**<0.001**	1.020

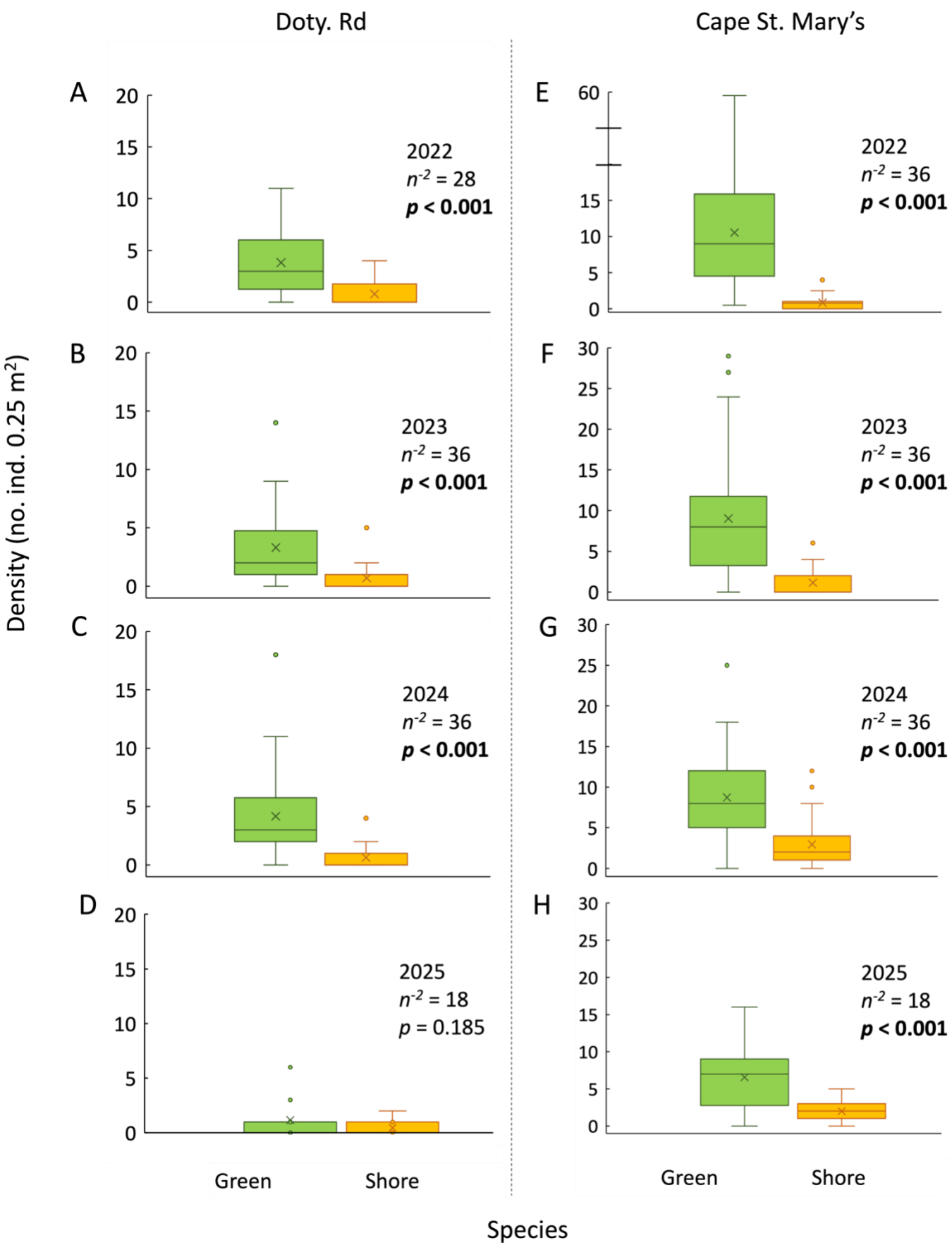
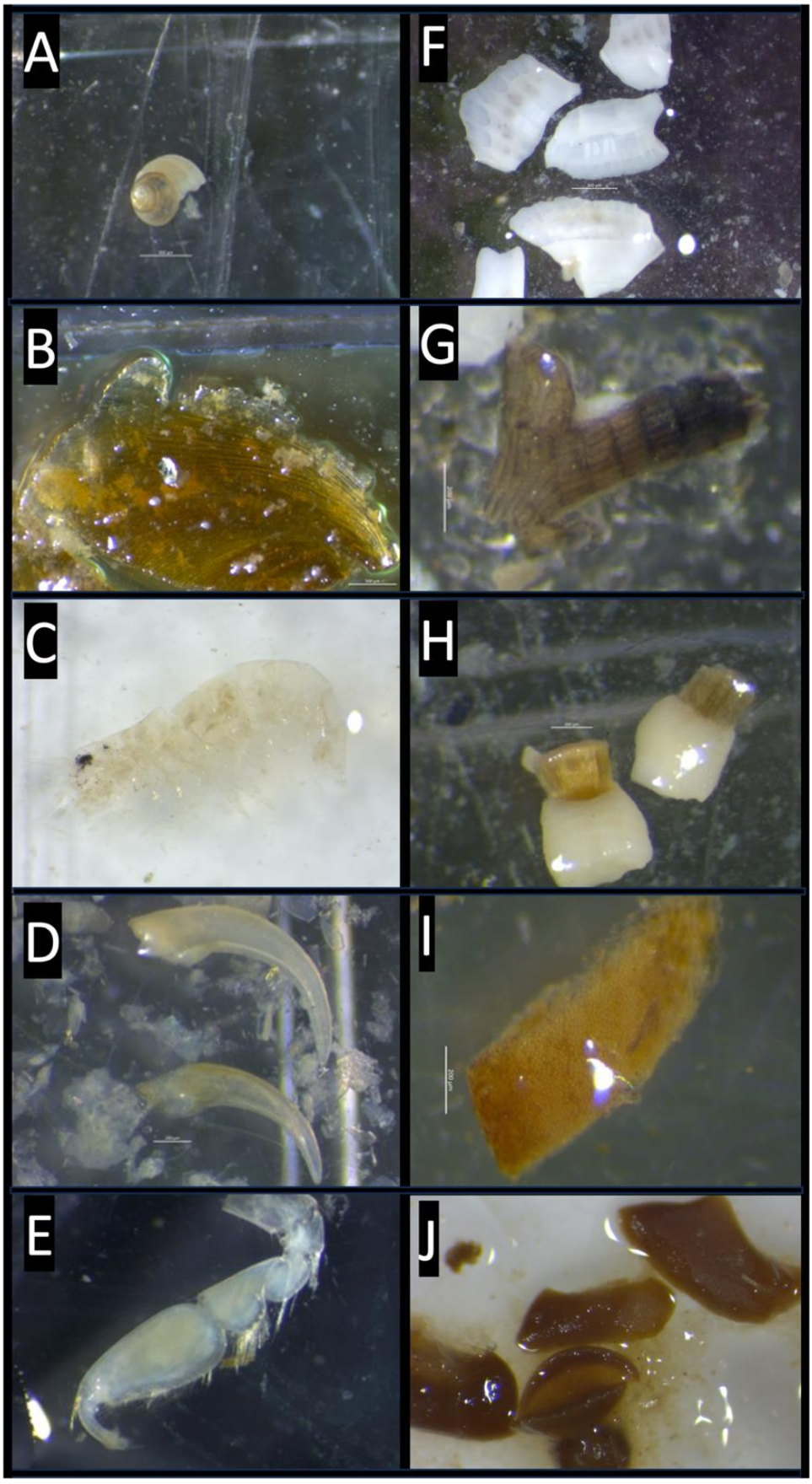

Doty. Rd
Cape St. Mary's
A
B
C
D
E
F
G
H
2022
n^{-2} = 28
p < 0.001
2023
n^{-2} = 36
p < 0.001
2024
n^{-2} = 36
p < 0.001
2025
n^{-2} = 18
p = 0.185
2022
n^{-2} = 36
p < 0.001
2023
n^{-2} = 36
p < 0.001
2024
n^{-2} = 36
p < 0.001
2025
n^{-2} = 18
p < 0.001
Density (no. ind. 0.25 m²)
Green
Shore
Green
Shore
Species

Figure 5. Box-and-whisker plots comparing green (green bar) and shore crab (orange bar) densities (number of individuals 0.25 m^{-2}) at two sites (Doty Rd., left panel; Cape St. Mary's, right panel) in July/August of 2022 to 2025. *n* values (shown in each panel) indicate the number of 0.5 x 0.5 m quadrats sampled. The line dividing the box in half is the median and the X indicates the mean. The vertical spread of the box indicates the interquartile range, encompassing the middle 50% of the data. Dots denote outliers. Bold *p*-values represent significant differences between green and shore crab densities for each site/year. Note y-axis differs among panels.

Diet

Both crabs consumed a wide variety of food items (Figure 6). Specifically, 23 taxonomic groups were initially identified in both crabs' stomach content; however, after the removal of stomachs with < 1 square of food (classified as empty stomachs), as well as the removal of food items that were not found in more than 10 stomachs, 12 taxonomic groups (Table 5) remained and were used for the diet analyses. Out of all crabs collected, 25% and 34% of green and shore crabs had empty stomachs, respectively. Principal Coordinate Analysis (PCO) analyses of the proportion of different species/taxa observed in crab stomachs at Doty Rd. and Cape St. Mary's in 2022 (Figure 7A) and 2023 (Figure 7B) explained in 51% and 61% of the total variability in the data, respectively. In 2022, a permutational multivariate analysis of variance (PERMANOVA) indicated significant differences in stomach content among sex, species, and site with significant sex x species and species x site interactions (Table 6; Figure 7A, B, Figure 8). Post-hoc tests for significant interactions are shown in Table 7; however, the significant difference in stomach content between green and shore crabs at Doty Rd. in 2022 must be interpreted with caution, as the sample size was relatively unbalanced and PERMDISP indicated significant overdispersion. In 2023, differences in stomach content composition varied among species, and sites with no interaction (Table 8). Four species/taxonomic groups, including barnacles (*Semibalanus balanoides*), crustacean spp., and brown macroalgae (*Fucus* spp.), and green macroalgae, were most important (Pearson correlation ± 0.6) in driving the observed differences in crab stomach content among species and sites. Green crab stomachs contained a relatively high proportion of animal prey (i.e., barnacle at Doty Rd. 2022/2023 and crustacean spp. at Cape St. Mary's 2022) compared to macroalgae (Figure 9A–C), except at Cape St. Mary's in 2023, where they had a more even proportion of animal prey and green macroalgae in

their stomachs. Shore crab stomachs showed the opposite pattern at Cape. St. Mary's, containing a relatively high proportion of macroalgae compared to animal prey (Figure 9C, D), but not at Doty Rd., where they had a relatively high proportion of barnacles in their stomachs (Figure 9A, B).


A
F
B
G
C
H
D
I
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J

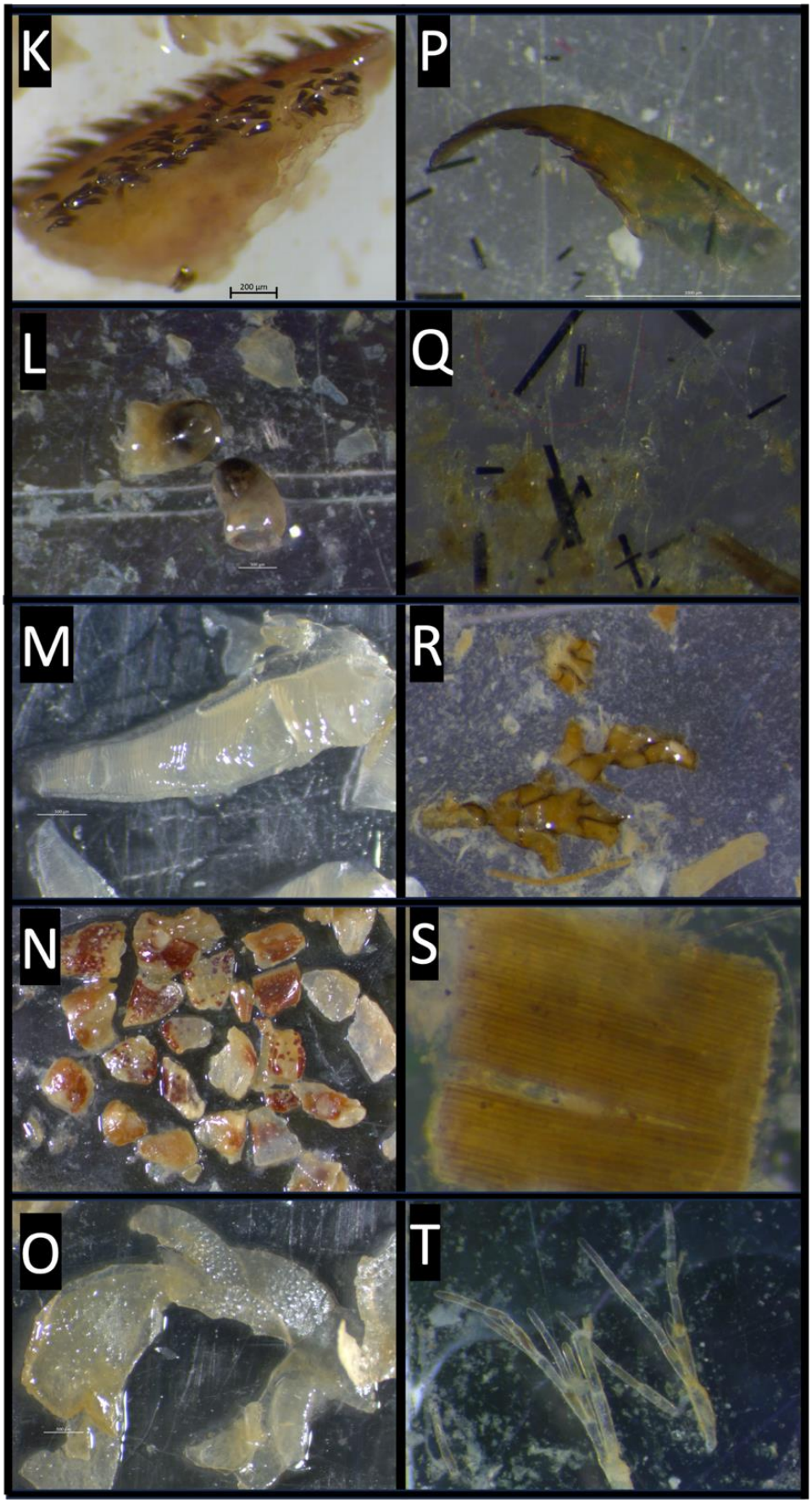
K
200 µm
P
L
Q
M
R
N
S
O
T

Figure 6: Figure plate of identifiable food items found in crab stomachs. Complete gastropod shell (A), gastropod operculum (B), *Gammarus* spp. (C), amphipod gnathopod claws (D), amphipod appendage (E), *Semibalanus balanoide*s (F), *Polysiphonia lanosa* (G), *Corallina officinalis* (H), *Fucus* spp. (I and J), setae on crab appendage (K), crab eyes (L), crab gills (M), *Hemigrapsus sanguineus* carapace (N), *Carcinus maenas* carapace (O), polychaetae jaw (P), setae (*Nereis* spp; Q), *Dynamena* spp. (R), *Ammophila* spp. (S), and unknown green algae (T). Pictures captured on ZEISS stereomicroscope using ZenPro image analysis software.

Table 5: List of 12 recognizable food items in the stomach content of green and shore crabs, with the distinguishing features used to identify them taxonomically. Food items listed were found in at least 10 stomachs.

Food item	**Distinguishing feature(s)**
Barnacle (*Semibalanus balanoide*s)	Fragments, cirri appendages
Crustacean	Carapace pieces (fragments), appendages
	e.g., amphipod (*Gammarus* spp.); Gnathopod claws, appendages, whole organism
	e.g., crab (*Hemigrapsus sanguineus* and *Carcinus maenas*); carapace, appendages, gills
Gastropod	Whole shell, operculum
Polychaetae	Setae, jaws
Calcareous red algae (*Corallina officinalis*)	Fragments
Sea truffle (*Polysiphonia lanosa*)	Fragments
Green algae	Fragments
Brown algae	Fragments
Cord grass (*Ammophila* sp.)	Fragments
Unknown vegetation (1)	Fragments
Unknown vegetation (2)	Fragments
Unknown vegetation (3)	Fragments

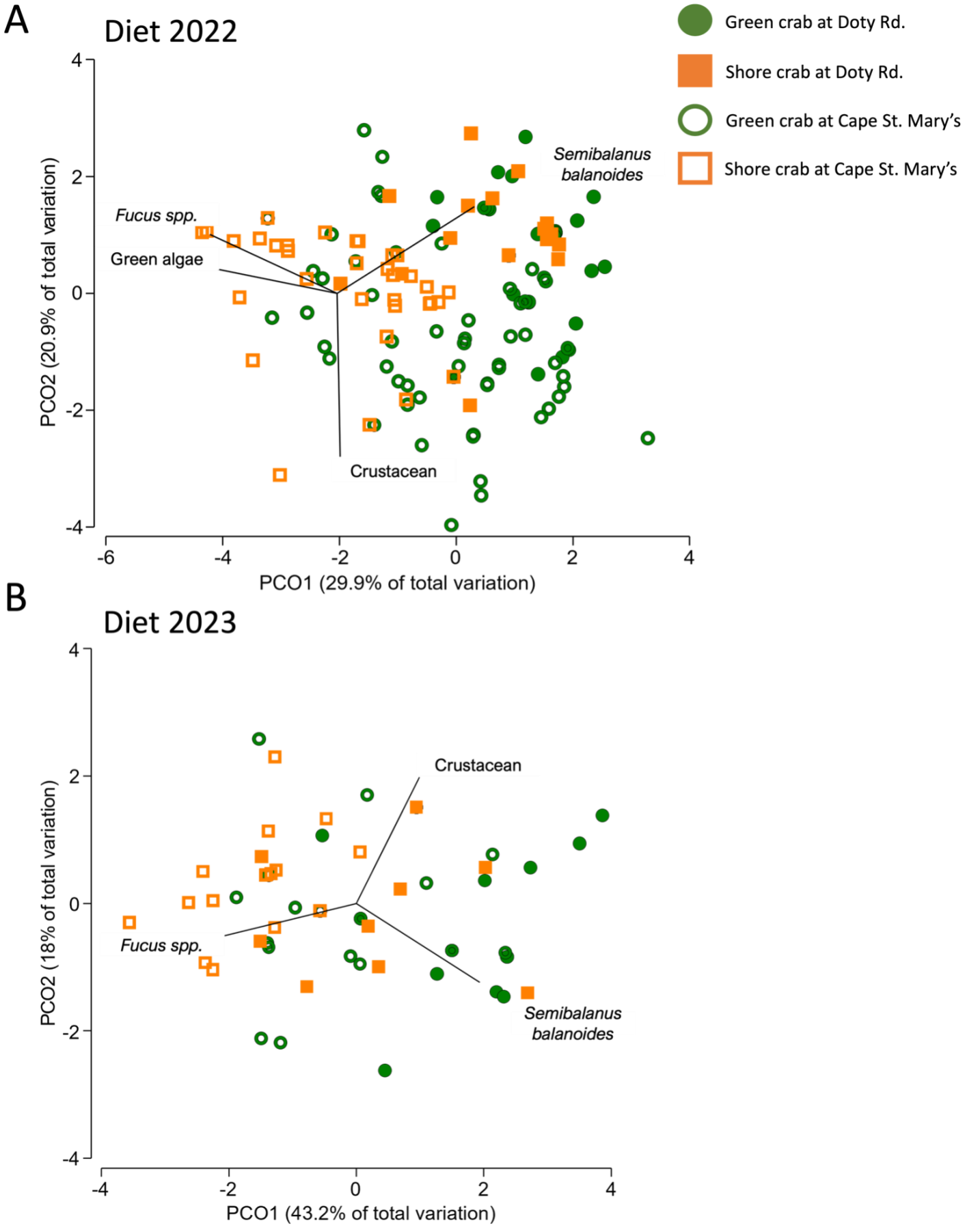
A
Diet 2022
Green crab at Doty Rd.
Shore crab at Doty Rd.
Green crab at Cape St. Mary's
Shore crab at Cape St. Mary's
Semibalanus balanoides
Fucus spp.
Green algae
Crustacean
PCO2 (20.9% of total variation)
PCO1 (29.9% of total variation)
B
Diet 2023
Crustacean
Fucus spp.
Semibalanus balanoides
PCO2 (18% of total variation)
PCO1 (43.2% of total variation)

Figure 7. Principal Coordinate Analysis (PCO) of crab stomach content (i.e., based on proportion (%) of species/taxon composition of food items) in 2022 (A) and 2023 (B). Vector overlays show species/taxa most important in driving the observed differences in crab stomach content among species and sites (based on Pearson correlation ± 0.6). Green crabs (2022): Doty Rd. n = 49/ Cape St. Mary's n = 67; Shore crabs (2022): Doty Rd. n = 17/ Cape St. Mary's n = 30. Green crabs (2023): Doty Rd. n =16 / Cape St. Mary's n = 21; Shore crabs (2023): Doty Rd. n = 9/ Cape St. Mary's n = 18.

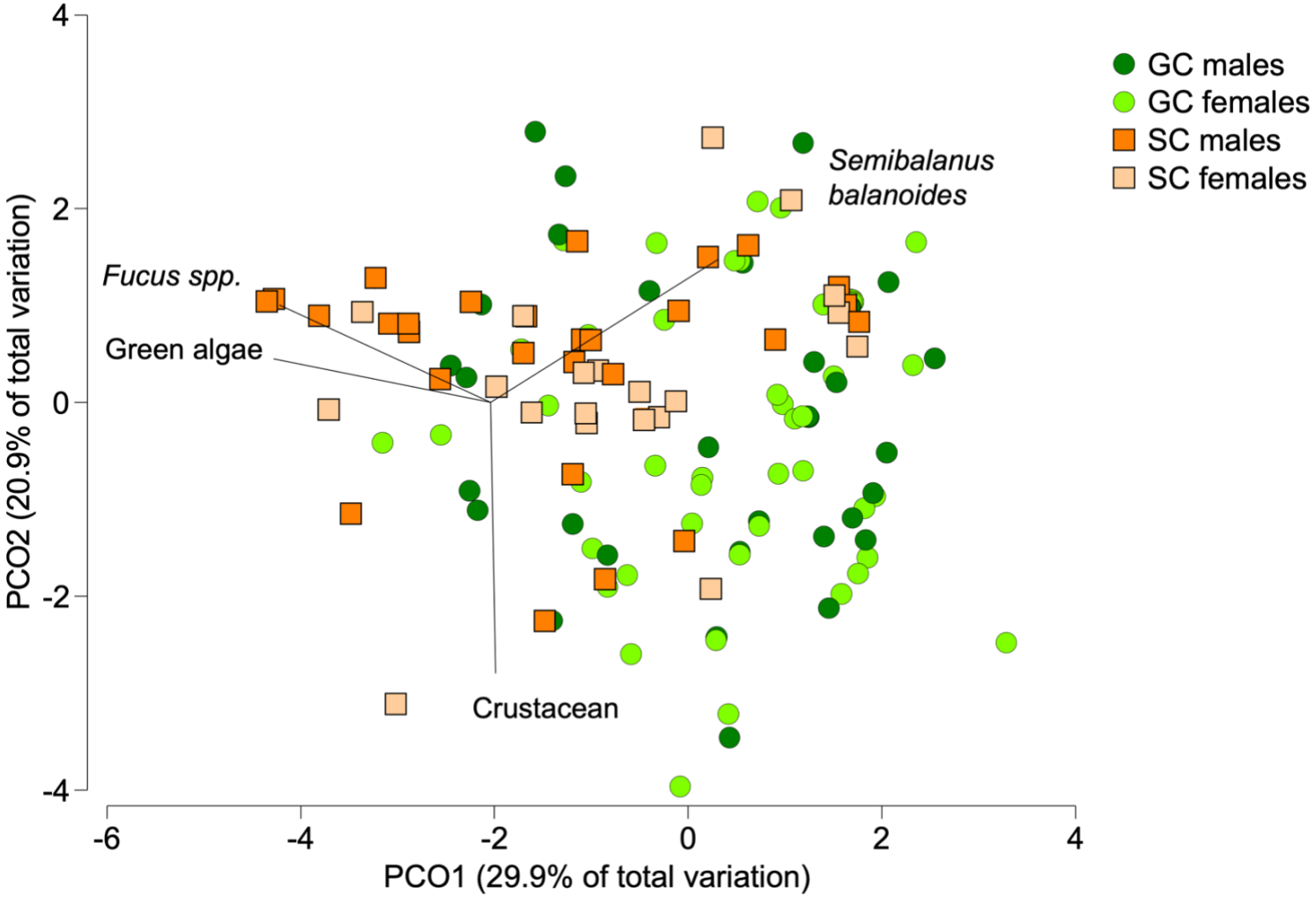

Figure 8: Principal Coordinate Analysis (PCO) of crab stomach content (i.e., based on proportion (%) of species/taxon composition of food items) of male and females of both green and shore crabs (GC and SC, respectively) in 2022. Vector overlays show species/taxa most important in driving the observed differences in crab stomach content among sex and species (based on Pearson correlation ± 0.6).

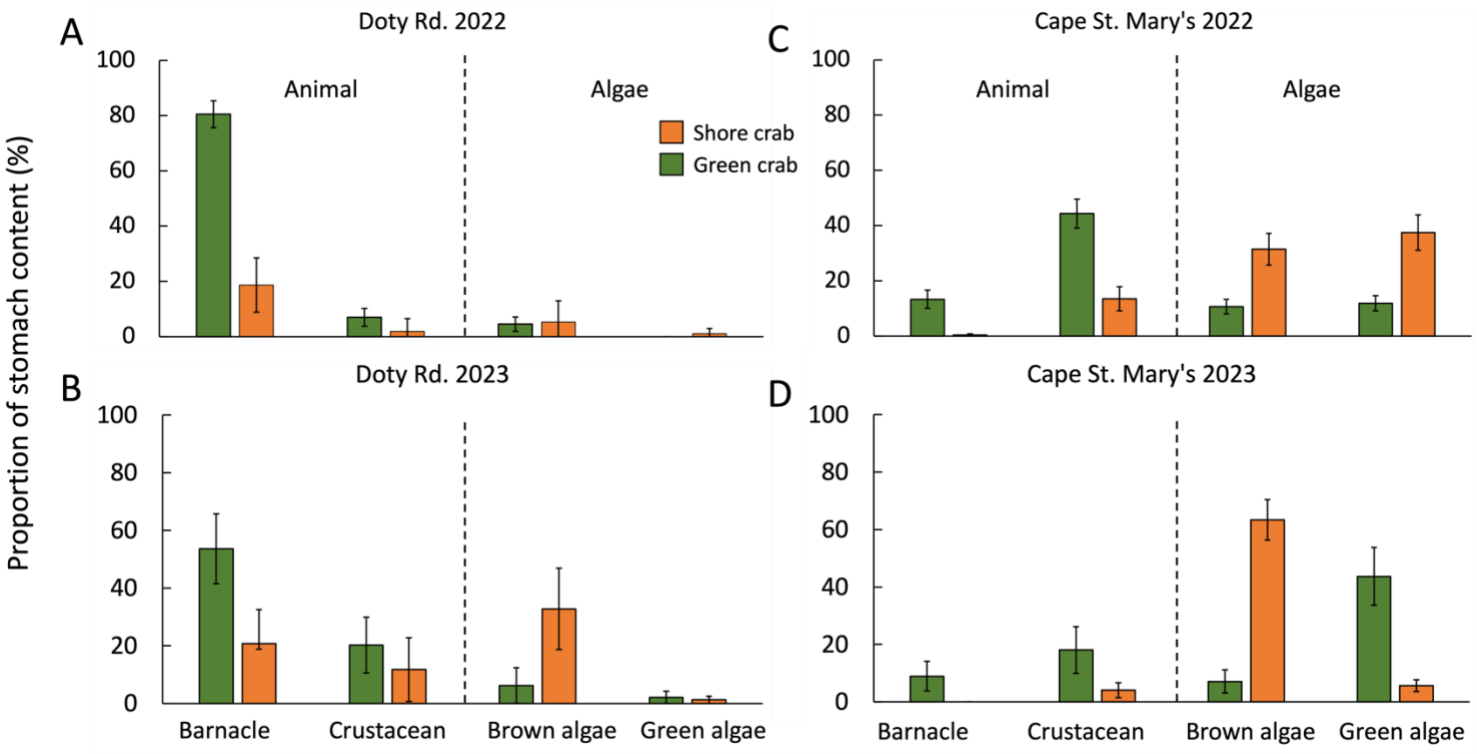

Figure 9. Proportion (mean ± SE) of species/taxa found in green (green bars) and shore crabs (orange bars) stomachs at Doty Rd. (A and B) and Cape St. Mary's (C and D) in 2022 and 2023 (species/taxa shown are based on Principal Coordinates Analyses; Pearson correlation ± 0.6). Green (2022): Doty Rd. n = 49/ Cape St. Mary's n = 67; Shore (2022): Doty Rd. n = 17/ Cape St. Mary's n = 30. Green (2023): Doty Rd. n = 16/ Cape St. Mary's n = 21; Shore (2023): Doty Rd. n = 9/ Cap St. Mary's n = 18.

Table 6. Results of three-way crossed Permutational Multivariate Analysis of Variance (PERMANOVA) testing for differences in crab stomach content for 2022 (n = 171) between sex (male and female), species (shore and green crab), and site (Doty Rd. and Cape St. Mary's) including interactions. Significant effects are shown in bold.

Source of variation	**dF**	**SS**	**Pseudo-F**	***p*-value**	**Variance explained (%)**
Sex	1	16.8	2.69	**<0.018**	1.2
Species	1	71.9	11.49	**0.0001**	5.2
Site	1	161.7	25.84	**0.0001**	11.6
Sex x Species	1	14.1	2.25	**0.0425**	1.0
Sex x Site	1	7.7	1.23	0.2923	0.5
Species x Site		33.4	5.34	**0.0003**	2.4
Sex x Species x Site	1	7.4	1.19	0.3344	0.5
Residuals	163	1020.2			73.1
Total	170	1394.8			

Table 7. Pairwise Permutational Multivariate Analysis of Variance (PERMANOVA) post-hoc comparisons for significant interaction terms (Table 6) examining differences in crab stomach content for 2022.

Group	**Comparison**	***t***	***p*-value**
Green	male vs. female	1.1097	0.299
Shore	male vs. female	1.6265	**0.0193**
Male	green vs. shore	2.4714	**0.0003**
Female	green vs. shore	2.7617	**0.0001**
Green	Doty Rd. vs. Cape St Mary's	4.4217	**0.0001**
Shore	Doty Rd. vs. Cape St Mary's	3.5515	**0.0001**
Doty Rd.	green vs. shore	2.3645	**0.0002**
Cape St. Mary's	green vs. shore	3.7831	**0.0001**

Table 8. Results of three-way crossed Permutational Multivariate Analysis of Variance (PERMANOVA) testing for differences in crab stomach content for 2023 (n = 64) between sex (male and female), species (shore and green crab), and site (Doty Rd. and Cape St. Mary's), including interactions. Significant effects are shown in bold.

Source of variation	**dF**	**SS**	**Pseudo-F**	***p*-value**	**Variance explained (%)**
Sex	1	7.6	1.5	<0.195	1.9
Species	1	26.9	5.3	**0.0002**	6.7
Site	1	52.0	10.2	**0.0001**	12.9
Sex x Species	1	5.9	1.2	0.3299	1.5
Sex x Site	1	1.3	0.26	0.9096	0.3
Species x Site	1	1.4	0.28	0.8971	0.3
Sex x Species x Site	1	4.3	0.84	0.5332	1.1
Residuals	56	285.0			70.9
Total	63	401.7			

Species interactions

A Generalized Linear Model showed that the presence of food in crab stomachs did not differ between species or treatments (Table 9; Figure 10A); however, there was a significant difference in the presence of barnacles ($X^2 = 6.569$, $p = 0.010$; Figure 10B) and macroalgae ($X^2 = 4.564$, $p = 0.033$; Figure 10C) in stomach contents between shore crabs and green crabs, with no effect of treatment (Table 9). The likelihood of barnacles being present was greater for green crabs, whereas the likelihood of macroalgae being present was greater for shore crabs. Additionally, a Generalized Mixed Model showed that the likelihood of different food items (barnacle vs. macroalgae) being present in stomach contents varied in green crabs ($X^2 = 8.733$, $p = 0.003$), but not shore crabs (Table 10). Planned comparisons indicated that green crabs were more likely to have barnacles present when alone ($p = 0.008$) and with a conspecific ($p = 0.011$), but not when paired with a shore crab (Figure 11B; Table 10), such that in heterospecific treatments they were equally as likely to consume either food item (Fig. 11A, 12A). Overall, green crabs showed a decreasing trend in barnacle consumption across treatments (alone, conspecific, heterospecific), with a corresponding increase in macroalgae consumption (Figure 11A, 12A). Shore crabs also showed reduced barnacle consumption in heterospecific treatments, but without a corresponding increase in macroalgae, and their overall diet remained relatively even across treatments (Figure 11B, 12B). The highest proportion of empty stomachs in shore crabs was observed in heterospecific treatments (54%), compared with when alone (26%) or with a conspecific (38%). In contrast, the proportion of empty stomachs in green crabs remained relatively consistent across treatments (29% alone, 36% conspecific, 39% heterospecific).

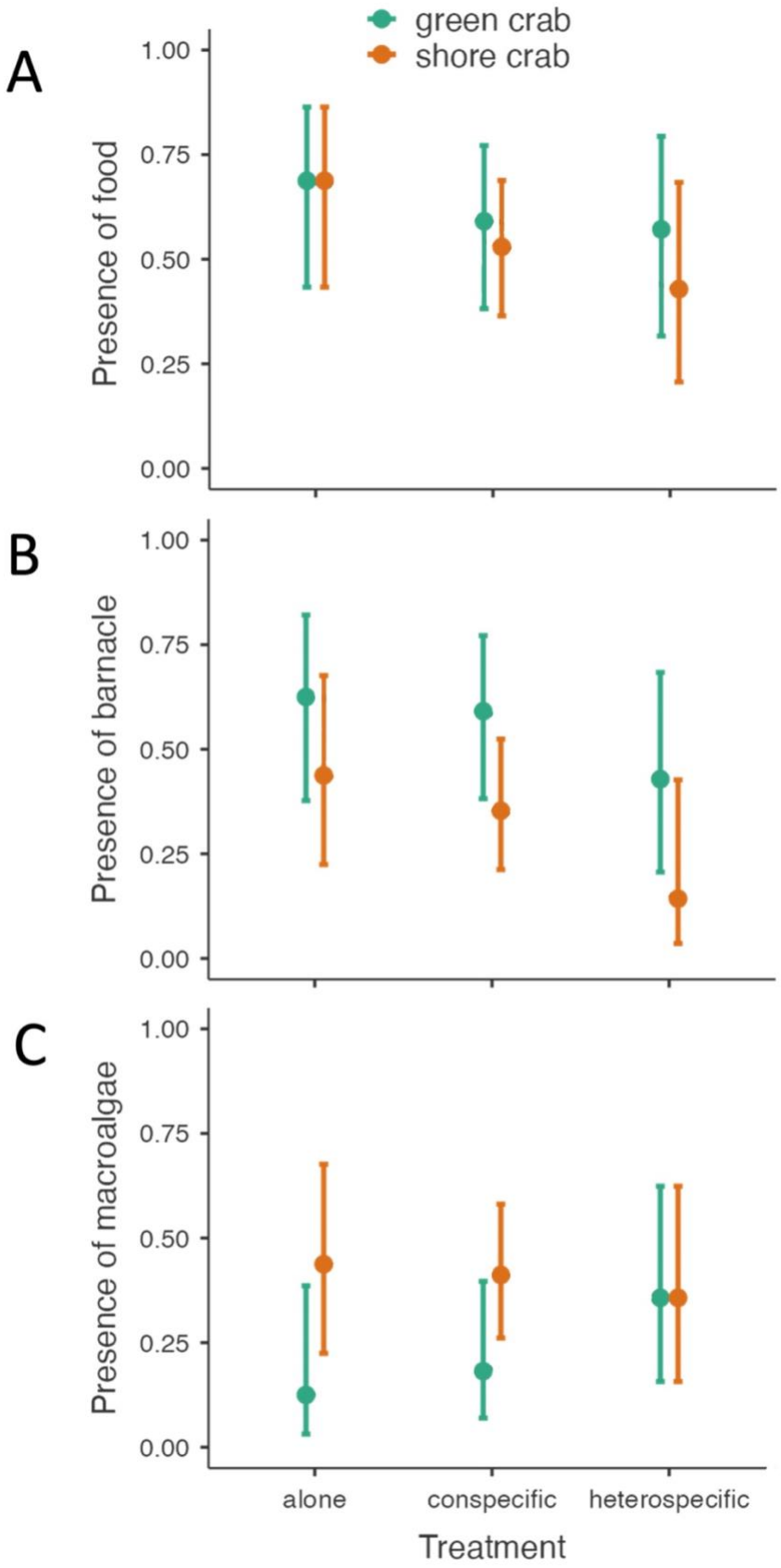
A
B
C
green crab
shore crab
Presence of food
Presence of barnacle
Presence of macroalgae
1.00
0.75
0.50
0.25
0.00
alone
conspecific
heterospecific
Treatment

Figure 10: Likelihood of the presence of (A) food, (B) barnacle, and (C) macroalgae in the stomachs of green (green symbols) and shore crabs (orange symbols) across the three treatments (alone, conspecific pair, heterospecific pair). Values represent predicted mean probabilities from Generalized Linear Models (binomial distribution, logit link), with error bars indicating 95% confidence intervals.

Table 9: Summary of Generalized Linear Model results examining the effects of treatment, species, and their interaction on the presence of food, barnacle, and macroalgae in crab stomachs. Reported values are *p*-values, chi-square test (X^2), and degrees of freedom (df).

Response variable	**Independent variable**	***p*-value**	X^2	**df**
Presence of food	Treatment	0.307	2.361	2
	Species	0.496	0.464	1
	Treatment*Species	0.866	0.287	2
Presence of barnacle	Treatment	0.099	4.620	2
	Species	**0.010**	6.569	1
	Treatment*Species	0.813	0.413	2
Presence of macroalgae	Treatment	0.671	0.799	2
	Species	**0.033**	4.564	1
	Treatment*Species	0.324	2.253	2

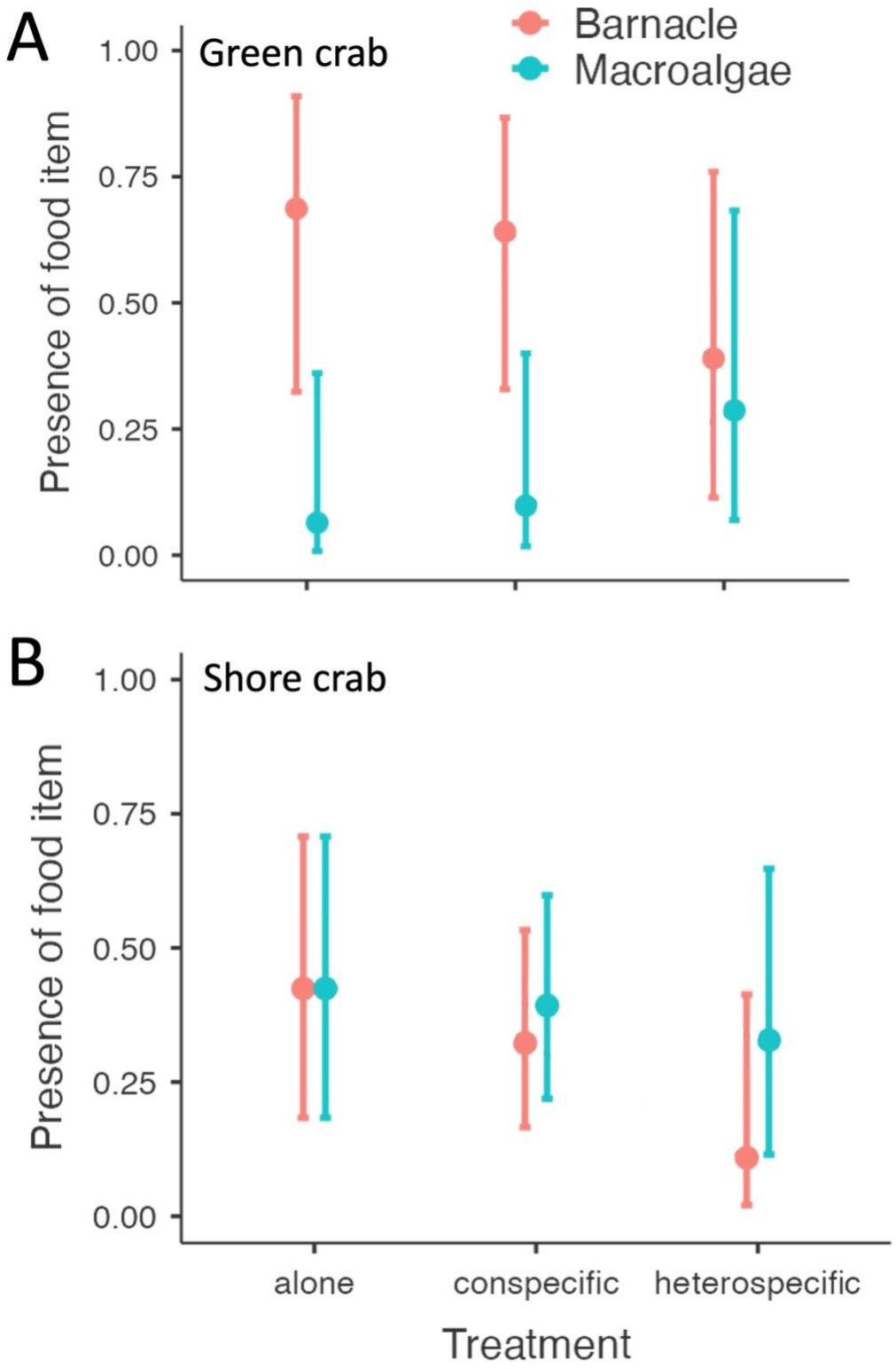
A
Green crab
Barnacle
Macroalgae
Presence of food item
1.00
0.75
0.50
0.25
0.00
B
Shore crab
Presence of food item
1.00
0.75
0.50
0.25
0.00
alone
conspecific
heterospecific
Treatment

Figure 11: Likelihood of different food items being present in green crab (A) and shore crab (B) stomachs with food items categorized as presence/absence of barnacle (pink symbol) and macroalgae (blue symbol) across three treatments (alone, conspecific pair, heterospecific pair). Values represent predicted mean probabilities from generalized mixed models (binomial distribution, logit link, crab IDs as random effects on intercepts), with error bars indicating 95% confidence intervals.

Table 10: Summary of Generalized Mixed Model results examining the effects of treatment, food type, and their interaction on the presence of food types in stomachs of shore crabs and green crabs. Reported values are *p*-values, chi-square test, and degrees of freedom for each response variable. Includes post-hoc tests.

Species	**Independent variable**	***p*-value**	X^2	**df**
Green crab	Food type	**0.003**	8.733	1
	Treatment	0.960	0.083	2
	Food type*Treatment	0.129	4.102	2
Shore crab	Food type	0.231	1.430	1
	Treatment	0.321	2.270	2
	Food type*Treatment	0.543	1.220	2
Planned comparison	**Comparison**		**z**	***p*-value**
Green Crab	Alone: Barnacle vs. Macroalgae		2.67	**0.008**
	Conspecific: Barnacle vs. Macroalgae		2.53	**0.011**
	Heterospecific: Barnacle vs Macroalgae		0.48	0.634

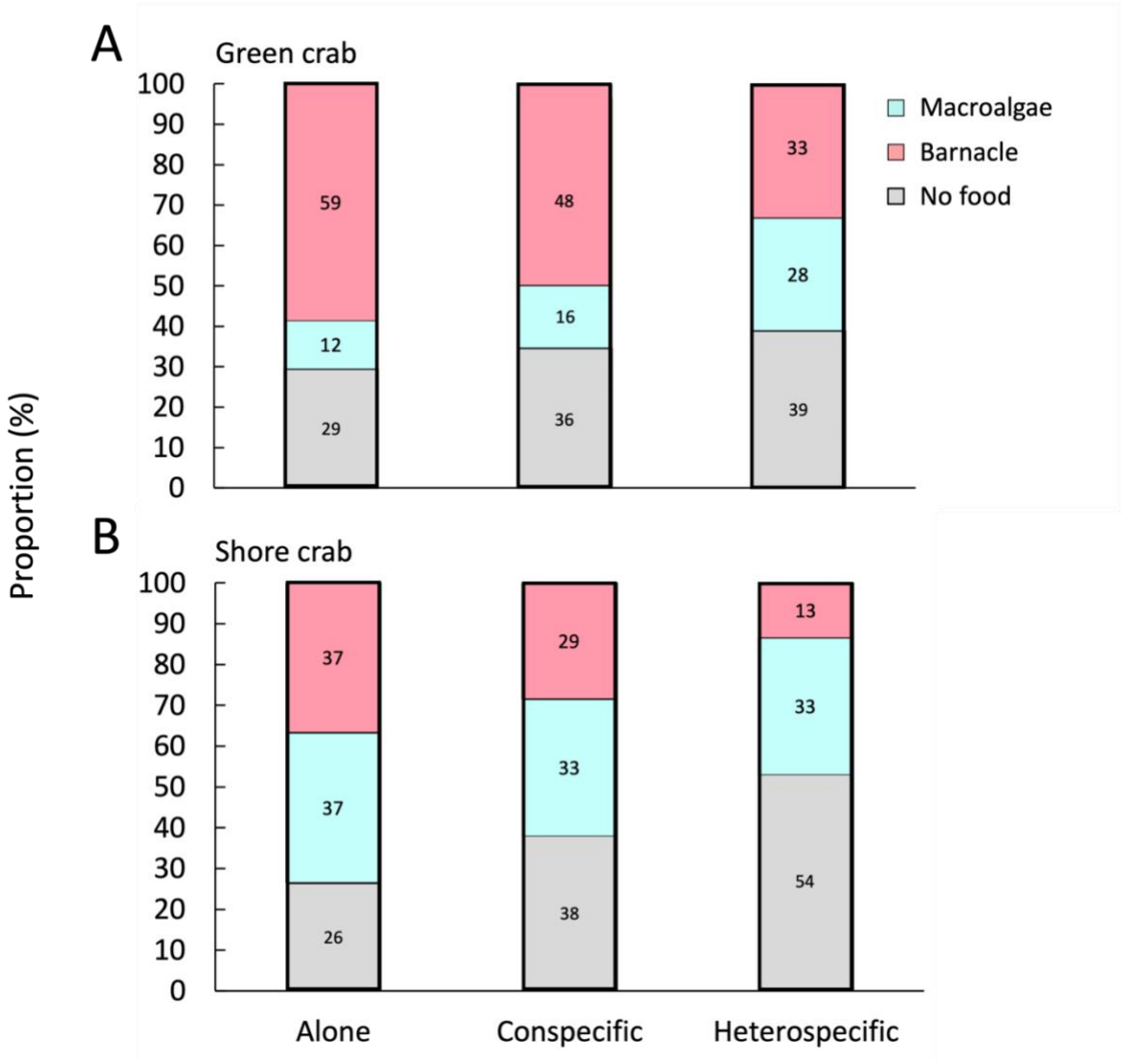

Figure 12. Proportion of green crab (A) and shore crab (B) stomachs by diet category, shown as stacked bars, across treatments (alone, conspecific, and heterospecific). Diet categories include no food (grey), macroalgae (blue), and barnacle (pink). Numbers within bars indicate proportion (%).

Discussion

Fine scale patterns of co-occurrence and abundance

This research provides the first examination of the shore crab's stage of invasion at two sites in the inner and outer regions of St. Mary's Bay, NS, since it was first observed there ~8 years ago in 2017. Based on the statistical classification scheme proposed by O'Connor (2014), which examined trends in the relative abundance of co-occurring invasive green and shore crabs over 12 years in New England, the higher densities of green crabs compared to shore crabs in NS over the summers of 2022 to 2025 indicate that shore crabs are still at the early stage of invasion at the two locations examined. The only exception was at Doty Rd. in 2025, where similar densities of these two species indicate that the shore crab may have entered the middle invasion stage. Although O'Connor did not indicate the duration of the early stage of invasion, shore crabs were first observed in Massachusetts in 1992 (McDermott 1998), and the mid-stage was reached by ~2000–2001 (O'Connor 2014), suggesting the early stage may last ~8–9 years. Given these results, it is conceivable that the shore crab may be in the middle stage of invasion at Doty Rd; however, continued sampling in NS is needed to determine if this is the case or whether the 2025 data simply represent interannual variability. Moreover, based on O'Connor (2014), the middle stage of invasion (i.e., no significant differences in either species densities) generally persisted for < 0.5 to 2.5 years before shore crabs became significantly more abundant than resident species, including the invasive green crab. Therefore, monitoring over the next few years in NS will be critical to capture this possible transition and determine whether it follows a pattern similar to what described by O'Connor (2014) as local community composition and environmental conditions likely influence invasion progression.

In both their native and invaded ranges, these crabs use rocky cobble substrate (Fukui 1988; Jensen et al. 2002) to avoid predation and desiccation (Kraemer et al. 2007). Shore crabs, however, appear more dependent on rock crevices for shelter, whereas green crabs can also bury themselves in sand (Jensen et al. 2002). Green crabs exhibit greater habitat flexibility, occupying subtidal mudflats, sandflats, and rocky areas (MacDonald et al. 2018), whereas shore crabs are largely restricted to rocky habitats (Lohrer and Whitlatch 2002a). In NS, shore crabs and green crabs were observed utilizing similar habitat in the mid-high rocky intertidal zone, residing close together within an area of <0.25 m^2. It was generally uncommon to find either species residing alone or the shore crab residing with a conspecific. In contrast, aggregations of conspecific green crabs and heterospecific individuals were similarly frequent; however, interpreting occurrence without considering species' abundances can be misleading. The higher densities of green crabs at both sites in most years likely contributed to the elevated frequency of green crab aggregations with conspecifics and heterospecific individuals, especially given both species' preference for structurally complex habitats (i.e., rocky cobble; Hobbs et al. 2017). To account for this, co-occurrence data were analyzed to determine whether observed patterns differed from random expectations based on crab abundances. Across all years, both species were more likely to occur alone than expected by chance (for shore crabs at Doty Rd. only), while aggregations of conspecific green crabs and heterospecific individuals were less frequent than expected (at both sites) (P. Ramey-Balci, personal communication; Standardized Effect Sizes, SES). These results suggest that although relative abundance may influence aggregation, non-random factors such as species interactions are likely important in shaping patterns of co-occurrence. Indeed, field surveys from Massachusetts to Maine indicate that density patterns across spatial scales reflect negative species interactions (Griffen et al. 2008).

Although co-occurrence does not necessarily indicate interaction (e.g., interference competition), small spatial overlap is required for direct interactions to occur (Galiana et al. 2024), and competition for shared use of resources such as optimal habitat would likely increase if shore crab populations grew. Moreover, the ability of an invader to outcompete both native and other invasive species for habitat and shelter is an important determinant of invasion success (Parker et al. 1999; Hobbs et al. 2017). Previous research suggests that habitat use by green crabs can be strongly influenced by interspecific interactions with shore crabs. Both experimental and field studies have demonstrated that competition with shore crabs can reduce green crab use of rocky intertidal habitats, forcing individuals into alternative microhabitats (Jensen et al. 2002; Lohrer and Whitlatch 2002a); however, despite declines in invasive green crab populations in rocky intertidal habitats associated with increasing numbers of shore crabs in the United States, both species continue to co-exist, possibly due to high resource availability (e.g., shelter and food), which can reduce competition and facilitate coexistence (Griffen et al. 2008; Gehrels et al. 2016; Móréh et al. 2024). The ability of an invader to outcompete both native and other invasive species for habitat and shelter is an important determinant of invasion success (Parker et al. 1999; Hobbs et al. 2017). In addition, the quality and quantity of available food resources are also important factors in the successful establishment and continued spread of an invasive species (Norris et al. 2007; Calizza et al. 2021; Reese et al. 2023).

Diet

I found that both species consumed a variety of animal and algal food items, consistent with studies indicating that both crabs are generalist omnivores (Portugal: Baeta et al. 2006, Hegoland: Saborowski 2023). Lab and field experiments in New Hampshire, USA, showed that diets consisting primarily of animal prey can result in a higher fitness (i.e., survival and reproductive output) compared to crabs feeding on readily available items such as macroalgae (manipulative field experiments: Griffen 2011; lab experiments: Belgrad & Griffen 2016). Low-quality diets can (i.e., macroalgae) influence crab populations by decreasing reproductive success (Griffen et al. 2011). Specifically, Griffen et al. (2011) conducted manipulative field experiments to assess diet and reproduction in invasive green crabs housed individually and exposed to different diets (e.g., animal vs. algal). Green crabs had lower energy stores and reduced gonad development when fed macroalgae. Another study by Griffen (2014) showed that increasing the daily amount of animal tissue consumed by green crabs resulted in an increase of ~5,200 eggs per 1% of their body weight, whereas consuming algae did not affect egg production (Griffen 2014). These findings suggest that access to animal prey over algal food sources may enhance the reproductive output of invasive crabs. This is especially significant, as dietary shifts towards macroalgae in green crabs have been experimentally observed when in the presence of the shore crab, both in the present study and in Griffen et al. (2008).

I found that animal prey was predominant in the green crab's stomach, whereas shore crabs tended to contain a relatively high proportion of macroalgae, with site and year-specific shifts towards more green algae consumption at Cape St. Mary's in 2023 for the green crab. My findings are consistent with other diet studies on crabs collected from various locations across the East Coast United States, which show that shore crabs are more herbivorous, with a higher

presence of macroalgae in their stomach content compared to green crabs (Griffen and Mosblack 2011). Moreover, Saborowski et al. (2023) found that native green crabs from Helgoland consumed more animal prey than invasive shore crabs, which primarily consumed macroalgae. Interestingly, morphological analysis of the gastric mill (the structure responsible for mechanical digestion in the cardiac stomach) of green and shore crabs further supports these dietary differences (Saborowski 2015). In Helgoland, the gastric mill of the native green crab is adapted for animal prey, with blunt, smooth ossicles suited for grinding soft tissue (Saborowski et al. 2023) and is therefore morphologically classified as carnivorous (Allardyce and Linton 2010). In contrast, the invasive shore crab has sharper gastric mill structures that facilitate cutting plant and algal material (Saborowski et al. 2023), supporting its classification as either herbivorous or omnivorous (Allardyce and Linton 2010). Applying similar morphological analyses to regions where both species are invasive would help determine whether the observed gastric mill differentiation is consistent across introduced ecosystems.

Co-occurring invasive species can also negative affect one another by one (or both) species preying on the other (Geburzi et al. 2018). Such species interactions can be inferred from an individual's diet (i.e., predation) (Dunne et al. 2002; Freilich et al 2018). Diet analyses also revealed, fragments of both crab species' carapaces in the stomach content of each species, indicating reciprocal predation on heterospecifics. Carapace identification in my thesis research was supported by preliminary feeding experiments, in which both species consumed smaller heterospecific juveniles (CW <12 mm), producing stomach content consistent with the observed fragments under stereomicroscopic examination. Lohrer and Whitlatch (2002a), also found that larger invasive shore crabs consumed smaller, invasive juvenile green crabs in laboratory experiments. Notably, Galiana et al. (2024) suggest that patterns at small spatial scales are more

likely to reflect local ecological interactions such as predation or competition, rather than shared habitat preferences alone. Together, my dietary analysis and quadrat sampling suggest that both crab species co-occur at fine spatial scales where direct species interactions are likely.

Interactions

Our results indicate that interspecific interactions had a stronger impact on both species than intraspecific ones. Shore crabs had the highest proportion of empty stomachs (53%) compared to green crabs (39%) during heterospecific treatments; however, interspecific interactions may have had a greater influence on green crab foraging and feeding behaviour than intraspecific interactions. Empty stomachs (i.e., starvation) may be worse than a dietary shift as starvation poses an immediate threat to survival, whereas shifting to a lower quality food source allows an organism to still maintain metabolic function and physiological processes, even if growth and reproduction are reduced (Griffen 2014; Belgrad and Griffen 2016). Notably, previous studies did not report the proportion or number of empty stomachs for either species, limiting direct comparisons and highlighting the importance of this metric in understanding competitive effects on feeding. Additionally, my results suggest that green crabs shift their diet in the presence of shore crabs, consuming a relatively higher proportion of algal material. This finding aligns with field experiments conducted by Griffen et al. (2008), which showed that when alone, green crabs had a greater stomach fullness and primarily consumed animal prey, but in the presence of shore crabs, stomach fullness was reduced and they shifted to a predominantly macroalgal diet (i.e., algae made up more than 50% of the stomach content). In contrast to my findings, Griffen and Williamson (2008), reported stronger effects of conspecific (green-green) than heterospecific (green-shore) interference on green crab feeding (primarily on *M. edulis*).

Future research should examine the effects of varying densities of conspecifics and heterospecifics, including both sexes, to evaluate the generality of these findings.

Dietary shifts such as observed here can have important consequences for individual fitness and population dynamics. Changes in diet can influence reproductive output, helping to explain how co-occurring invasive species affect each other's ability to colonize new habitats by indirectly affecting their population sizes (Griffen et al. 2008; Griffen et al. 2011; Griffen 2016). For example, declines in the abundance of green crabs along the Atlantic coast of the United States have been linked to reduced reproductive success associated with dietary shifts in the presence of shore crabs, as well as predation on juveniles by the shore crab (Lohrer & Whitlach 2002a; Griffen et al. 2011; Griffen 2016). Although crabs can compensate for low-quality diets by increasing their consumption, green crabs ultimately show reduced gonad development when their diet shifts toward a predominantly macroalgal diet (Griffen et al. 2008; Griffen et al. 2011).

Overall, shore crabs are still in the early stage of invasion in Nova Scotia, based on the sites I examined. Additionally, both crabs share similar habitat preferences for rocky cobble intertidal habitats and co-occur at small spatial scales, which are important for species interactions. Continued sampling at my sites would be crucial for monitoring the shore crabs' invasion through time, especially including other sites where shore crabs are known to have higher abundances than green crabs (pers. observation). Furthermore, my dietary analysis supports previous findings that these crabs are generalist omnivores; however, they display species-specific food preferences for animal prey (green crab) and macroalgae (shore crab). Interestingly, in competition experiments, green crabs were significantly more likely to consume barnacle in alone and conspecific treatments, with no difference in consuming either food item in

heterospecific treatments. Future work should focus on videotaping my experiments to help reveal the mechanism behind the observed dietary shifts, rather than inferring it from feeding outcomes. Capturing these interactions would help distinguish between competition for resources (e.g., interference competition) and behavioural dominance (e.g., agonistic interactions), and provide the opportunity to quantify behaviours such as aggression frequency, time spent feeding, or displacement events.

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Appendix: Crab aggregation frequencies across all carapace width (CW) sizes

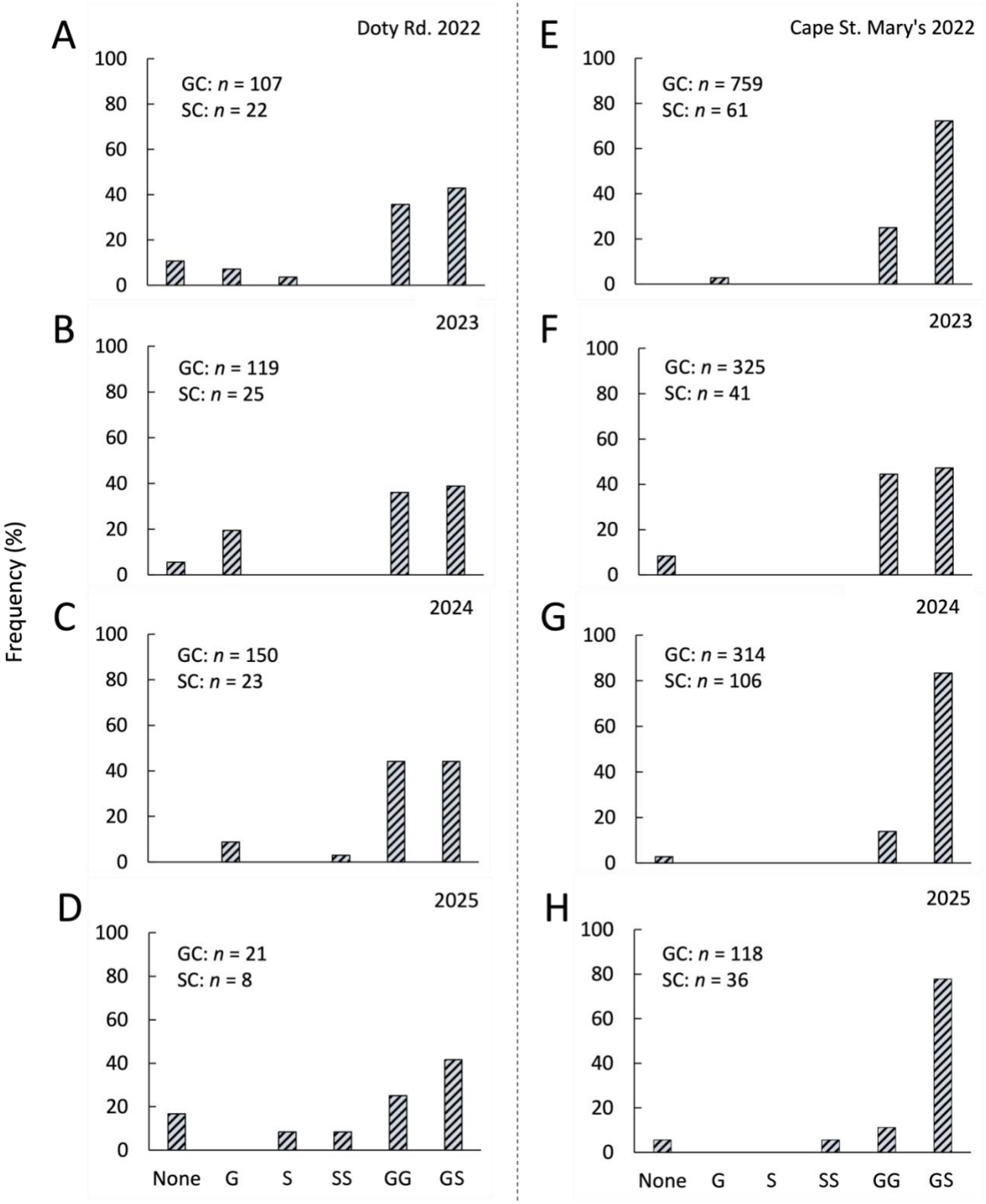

Figure 13. Frequency (%) of all crab occurrences in 0.25 m^2 quadrats by category at Doty Rd. (left panels) and Cape St. Mary's (right panels) in July/August of 2022 to 2025. Categories: none (no crabs), G (one green crab), S (one shore crab), SS (multiple shore crabs), GG (multiple green crabs), and GS (both green and shore crabs). Each panel includes total number (*n*) of green crabs (GC) and shore crabs (SC) collected during quadrat sampling. Table 1 indicates number of quadrats for each site/year.